XX. *On the Comparative Morphology of the Leaf in the Vascular Cryptogams and Gymnosperms.*

By F. O. Bower, *M.A., F.L.S.*

Communicated by W. T. Thiselton Dyer, *M.A., C.M.G., F.R.S.*

Received May 13,—Read May 29, 1884.

[Plates 37-40.]

Introduction.

The origin of the tendency among the earlier morphologists to draw a sharp distinction between stem and leaf may most probably be traced to the fact that vegetable morphology was first pursued as a science in regions where deciduous trees prevail. Seeing the leaves of so many plants fall off as a whole, while the scar left was almost a direct continuation of the external surface of the stem, doubtless gave rise to the view that the two should be regarded as radically distinct members.

As the science of morphology progressed it became necessary, if this distinction were to be maintained, to define more clearly how members belonging to these two categories differ one from another. Various attempts were made by authors to show in what the essential difference consisted, the most notable being that of Hofmeister,* who brought forward a number of distinctions, based chiefly upon development. The most essential of these were adopted in that section of the Text Book of Sachs,† which deals with the relations of leaves and leaf-forming axes. In the last paragraph (No. 8) of that section, he clearly lays down the principle that "the expressions *stem* and *leaf* denote only certain relationships of the parts of a whole—the *shoot.*" This principle is elaborated in his more recent lectures,‡ in which he writes as follows:—"A typical shoot consists of the leaves and the axis, which however are not really to be regarded as different organs, but fundamentally as parts only of *one* organ. . . . . . In their nature, and as shown by the history of their development, the leaves are fundamentally nothing more than processes, or outgrowths of the axis of the shoot. . . . . ." If we accept these propositions, and I do not see how we can do otherwise, the same method of morphological treatment

* Allgemeine Morphologie, pp. 406–416.

† Second English Edition, p. 153.

‡ Vorlesungen, p. 48.

should be applied to the leaf as is usual in studying the stem. On reading current morphological papers, however, it is very apparent that this is not done. Leaving out of account the use of that adhesive terminology, which constantly revives in the mind the older mode of viewing the leaf, it is still obvious that the treatment of the leaf by modern writers is different from that of the stem. Thus, to take as an example the best of the earlier works on leaf-development, viz., EICHLER's Dissertation on the Development of the Leaf;* after defining the *Primordial Leaf* as the young leaf before internal differentiation, or distinction of external parts, the author goes on to describe (p. 7) how the primordial leaf becomes differentiated into "two chief parts, which are common to the leaves of all Phanerogams, viz., a stationary zone, which takes no part in the further formation of the leaf, and a vegetative part which forms the lamina with its branches." The former he names the *foliar base* (blattgrund), and the products of its development are the sheath and the stipules if present; the latter he designates the *upper leaf* (oberblatt), which gives rise to the simple or branched lamina. The petiole is also, according to EICHLER (p. 8), derived from the upper leaf, though other more recent writers describe it as being intercalated between the two parts. This distinction first drawn by EICHLER has recently been revived, and the terminology, with some slight modifications, adopted by GOEBEL.† He has however imposed a very necessary limitation upon its application, viz.: that the two parts of the primordial leaf "are not sharply marked off from one another, but are only to be distinguished by the part which they play in the further growth of the young leaf." He has, on the other hand, extended it to the Monocotyledons and Gymnosperms, and occasionally also to certain Cryptogams, in which similar phenomena appear. Thus the distinction of the foliar base and upper leaf has become established in botanical terminology, and it is applied equally to both branched and unbranched leaves.

This distinction is a very natural outcome of the study of the development of the leaves of the higher plants, and it seems to lie ready to hand, but the comparison in this respect with the vascular plants, acknowledged to be lower in the scale, has been much neglected, and such a comparison should be made as a test of the validity of a distinction of this kind. Because it appears to be obvious in certain of the higher plants, the distinction is not necessarily valuable, nor even logical; while, as I shall point out later, it is not in conformity with the morphological method of treatment of the stem. The parts resulting from the development of the foliar base and upper leaf are, it is true, ready distinguishable from one another in certain of the higher plants, but the question is whether we draw this distinction between structures which are *morphologically coordinate*, and whether by distinguishing them we gain any further insight into the real nature of the leaf. It appears to me that

* EICHLER, Zur Entwickelungsgeschichte des Blattes. Marburg, 1861.

† Beitr. z. Morph. und Phys. des Blattes, Bot. Zeit., 1880, p. 753. Vergl. Entw. d. Pflanzenorgane, SCHENK's Handbuch, p. 215.

we do not, or at least not in all cases. I admit that no serious objection can be urged to applying this distinction of foliar base and upper leaf to simple, unbranched leaves, as in the Monocotyledons and Coniferæ, provided the parts develop in such a way as to warrant the distinction. But in leaves which are branched the case is different, and it may be stated that it was chiefly with such leaves that EICHLER was engaged when he first introduced the terms. When we distinguish between the foliar base and the upper leaf in a branch leaf, we divide the leaf into two parts which are not coordinate: on the one hand we place the basal part of the main axis of a branch-system, on the other the upper part of that axis *with its branches of all orders*. Such a distinction might be compared with that between the bole of a forest tree below the lowest branches on the one hand, and the whole of the upper part of the tree, including the upper part of the main axis together with its branches of all orders on the other. Such a treatment, though very obvious, can hardly be called scientific, and would not lead to a true insight into the morphology of the tree, such as might be obtained by following the main axis upwards, and tracing its identity from base to apex, and its relation to the branches, &c. It may have been thought that the peculiar conformations often found at the base of the leaf even in a comparatively early state of development would justify the distinction; but those peculiarities are the result of phenomena of distribution of growth of a nature which would not be allowed to be of sufficient morphological importance to justify such a distinction of parts in an axial branch system.

The most important point in the morphological study of a shoot or branch system is to ascertain the mode of origin and the sequence of appearance of the various parts, and their relations in these respects one to another; the greater importance being, as a rule, attached to those phenomena which are of earliest date. Thus, in treating of axes and branch systems, the time of origin, and the mode and point of first appearance are regarded as of greater morphological import than subsequent changes of conformation, brought about by peculiarities of the distribution and localisation of the intensity of growth, however greatly those changes may affect the general outline of the number or branch system. Thus in the common Hyacinth no radical distinction is drawn between the short lower part of the axis (the corm), which bears the scales of the bulb together with the foliage leaves, and the elongated part of the axis (the scape), which bears the flowers: both are recognised as parts of the same axis, though the difference in the distribution of the longitudinal growth in different parts of it is very great. Again, in certain shoots of *Vitis gongyloides*, of the Potato, &c., transverse growth is found to preponderate at certain points, resulting in the formation of fleshy swellings; but any morphologist, overlooking the results of excessive transverse growth, will still recognise in those structures a peculiar development of a part of the axis, which however still retains for him its identity throughout. Thus in treating of axes, morphologists recognise clearly that the mode of origin, and the mutual relations of members on their first appearance are

the most important points, and that, however much those relations may apparently be disturbed by various localisation of subsequent growth, the changes thus induced are to be regarded as but of secondary importance.

In dealing with the leaf this principle is not kept so clearly before the mind, and the explanation is doubtless to be found in the fact that the intercalary growth is usually localised, at or near the base of the leaf, at an earlier period than is the case in the stem. Current morphology still retains those obvious distinctions of sheath, petiole, and lamina, as coordinate structures, independently of the fact that the most salient and distinctive characters used in distinguishing these several parts one from another result from processes of growth in transverse and longitudinal directions, which, in the treatment of axes, would be freely admitted to be of but secondary importance, and certainly would not be allowed to take precedence of those phenomena of branching upon which the morphological treatment of the shoot is primarily based. In the leaf precedence is given to the more obvious results of intercalary growth, while the branching of the leaf is treated as of but secondary importance. This inconsistency demands further investigation. It must be ascertained by a comparative study of the leaf in forms acknowledged to be lower in the scale, whether there be sufficient reason for treating the leaf differently from the stem. It may be stated at once that in my opinion the comparative study of leaves of the lower vascular plants, which will be detailed below, does not justify such a difference of treatment.

Before bringing forward that mode of treatment of the leaf, which I shall propose as being more in accordance with the method of treatment of the axis, it will be necessary to say a few words on the subject of growth as affecting the external conformation of members.* Differences in direction, intensity, localisation, and duration of growth transversely to the organic axis of a member result in differences of its external form; and the forms which result may be roughly ranged in three series, though these graduate by intermediate forms one into another: (1) When the growth is equal in all directions transversely to the organic axis, the member is cylindrical. (2) When the growth along one transverse diameter is a maximum, and that in a diameter at right angles to it is a minimum, a flattened member is the result. In both the above cases the growth (exclusive of secondary changes) is usually nearly simultaneous over the whole cross-section. (3) When the growth is at first more or less uniform over the whole cross-section, but is subsequently localised, and continued more rapidly at one or more points at its periphery, variously winged members are the result. These three modes of development, as well as transitional forms between them, are to be found exemplified both among axes and leaves; but while the first is most common for axes, and most rare among leaves, the second and third are most common for leaves, and less usual for axes. It frequently happens that in one and the same axis there may be a gradual or even a comparatively sudden transition from one of these forms of development to another. Thus, in stems of *Rhipsalis*, *Coccoloba*, *Xylophylla*,

* Compare C. DE CANDOLLE, 'Théorie de la Feuille,' p. 19. Genève, 1868.

Ruscus, and *Phyllocladus*, one axis is frequently cylindrical below, and gradually more flattened above, yet no morphologist would lay any stress upon the distinction between the flattened part and the part which is cylindrical; both are regarded as parts of one and the same axis, though the transverse growth is not uniform throughout. It was, however, chiefly on the ground of an external conformation due to an unequal distribution of transverse growth, coupled with a "stationary" character,* that the distinction between *foliar base* and *upper leaf* was based; and this is not sufficient ground for distinguishing two categories which, as I have shown above, are not morphologically coordinate. If the shoot is to be treated uniformly and consistently, the treatment of the leaf must be modified.†

Instead of drawing the distinction, in the first instance, in leaves whether branched or unbranched, between the *foliar base* and the upper leaf, I propose to treat the whole leaf, from apex to base, consistently as a *podium*, or form of axis, which may or may not branch, and which may develop in different ways at different points. It will be necessary to define this podium by the use of a distinct term, which shall include not only a part of it, but the whole of it from apex to base, exclusive only of its branches.‡ Various words have been used by different authors, who have felt the necessity of defining this podium: thus "rachis" has been used, but this term has already another distinct application; the old term "midrib" has also been used, but this is unsatisfactory, since it implies that it is the rib which is at the middle of something, and this is not always the case, nor is it that character of the structure which it is desired to describe. I therefore propose the term *phyllopodium* to express the whole of the main axis of the leaf, exclusive of its branches, the word being similar in composition to the terms "sympodium," and "monopodium."

As is also the case with stem structures, the phyllopodium is capable of very various development. In the simplest examples it remains *unbranched*, and it may then develop (1) in a cylindrical manner, as in *Pilularia;* or (2) it may appear as a flattened structure without wings or midrib, as in *Welwitschia* and many Monocotyledons; or (3) it may be simply winged, through part or the whole of its length, as in *Gnetum*. In other cases the phyllopodium may branch, the branches being produced in acropetal or basipetal order: these may appear in the mature leaf as teeth at the margins of the wings, or as distinct *pinnæ*, which may themselves develop in various ways, and again branch, forming *pinnules*, and so on to higher orders of ramification.

As will be pointed out more at length at the close of this paper, the phyllopodium may develop uniformly throughout its length, as is the case in *Pilularia* and

* EICHLER, *l.c.*, p. 7. GOEBEL, Bot. Zeit., 1880, p. 759.

† EICHLER even goes so far as to argue (*l.c.*, p. 24), in answer to the opinion of MERCKLIN and others, who regarded stipules as basal pinnæ, that because the foliar base and upper leaf differ radically one from another, therefore members borne by them are not morphologically equivalent.

‡ Of course no sharp line can be drawn between its branches and itself, just as it is impossible to define accurately the limit between stem and leaf.

Welwitschia; in other cases by differences in the distribution of growth in tranverse and longitudinal directions, a different conformation may be acquired at different parts: thus a basal part or *hypopodium* may be recognised, which coincides with EICHLER'S "blattgrund": a median, elongated part, the *mesopodium*, which coincides with the petiole: and thirdly, an apical part, the *epipodium.**

It will be necessary to say a few words upon the third part of the phyllopodium, in order to show how it differs from the "oberblatt" of EICHLER, this being the essential point in which his method of treatment differs from that which I am endeavouring to establish. Under the term "oberblatt," EICHLER and GOEBEL include the whole of the upper part of the leaf whether branched or unbranched: supposing the leaf to be unbranched, the term "oberblatt" will include precisely the same part of the leaf as I wish to express by the term "epipodium." But in the case of branched leaves, while the term "oberblatt" will include the whole of the upper part of the leaf *with its branches,* in fact a whole branch-system, I should include under the term epipodium *only the upper part of the phyllopodium with its wings, and exclusive of its branches of higher order.* The difference of application of the terms may seem at first sight small, but beneath it lies an important difference of morphological method. By EICHLER the leaf is treated as one member, which may branch in its upper part; under the method which I propose it is treated throughout as a potential branch-system; under the former method a sharp distinction is drawn between the basal part of the leaf, and the upper part which may or may not branch; under the latter the distinction is between the podium, and the branches (if any) which it bears.

It seemed to me to be important to test the validity of my views as to the mode of procedure in studying the morphology of the shoot by a series of observations on those plants of the vascular series† which are universally allowed to be lowest in the scale, and this comparative study of the leaf seemed especially necessary, since it has been much neglected by those to whom we owe the chief advances in our knowledge of leaf-development. I had previously been engaged on the development of the leaves in the *Cycadaceæ* and *Gnetaceæ*, and thus a good opportunity was offered of working in the results obtained in those groups with those obtained by other writers and by myself in the vascular Cryptogams, so as to arrive at a comparative view of the development of the leaf in the whole series. It may be stated that the result of this comparative

* My reasons for introducing a new terminology are two. First, it is desirable to dispel as far as possible the idea upon which so much stress is laid by EICHLER, that there is an important difference between the "blattgrund," and "oberblatt" (*l.c.*, p. 25, "wesentlich von einander verschiedene Theile"): this may best be done by dropping his terms; secondly, while rejecting the general term "oberblatt" as expressing an idea which is not in accord with morphological method as applied to the axis, it is desirable to observe uniformity in the terminology.

† I purposely leave out of account the foliar *Muscineæ*, though these are so often used in comparison with vascular plants. It is often forgotten, while comparing the vegetative organs of *Muscineæ* with those of the vascular plants, that the structures compared are not *homologous*, but at best only *analogous* developments.

study is fully to justify the treatment of the whole leaf as a branch system, while it brings into greater prominence the fact that the main axis of the leaf in the more complicated forms has undergone a progressive differentiation as a supporting organ, as distinct from the branches of higher order which it bears; further, that as we pass upwards through the scale of vascular plants, there is a tendency to an earlier arrest of the apical growth of the phyllopodium; this, together with the increased prominence of the results of intercalary growth, which has in many cases so distorted the branching system of the leaf, gives a ready explanation of the origin of those methods of treatment of the leaf, which I have alluded to above.

Comparative Study of the Leaf.

Taking first that family of the Leptosporangiate Ferns* in which the simplest structure of the vegetative organs is represented, viz., the *Hymenophyllaceæ*, the phyllopodium is often found to be obviously winged throughout its length, and continuously to the point of insertion on the axis (*e.g.*, *Hymenophyllum ciliatum*, *Trichomanes radicans*),

* The term "*Leptosporangiate*" was first introduced by GOEBEL (Bot. Zeit., 1881, p. 717) to include those Ferns in which the sporangium originates from *one* cell; these are further distinguished by the whole structure of the sporangium, the regular succession of its cell divisions, the form of the archesporium, &c., from the *Eusporangiate* forms, in which the sporangium does not originate from a single cell, and is of more complicated structure. He puts forward the following classification:—

- I. *Leptosporangiate Forms.*
  - A. *Filices.*
    - (1) Homosporous Ferns. (Polypodiaceæ, Gleicheniaceæ, Cyatheaceæ, &c.)
    - (2) Heterosporous Ferns. (Salviniaceæ.)
  - B. *Marsiliaceæ.*
    - (1) Marsilia.
    - (2) Pilularia.
- II. *Eusporangiate Forms.*
  - A. *Filicales.*
    - (1) Marattiaceæ.
    - (2) Ophioglossaceæ.
  - B. *Equisetineæ.*
    - (1) Calamites.
    - (2) Equisetaceæ.
  - C. *Sphenophylleæ.*
  - D. *Lycopodinæ.*
    - (1) Lycopodiaceæ.
      - (*a*) Homosporous forms. Genus Lycopodium.
      - (*b*) Heterosporous forms. Lepidodendron. Sigillaria (?)
    - (2) Psilotaceæ.
    - (3) Selaginelleæ.
    - (4) Isoetæ.
  - E. *Gymnosperms.*

while in other cases the winging is less marked, but still traceable (*Trichomanes Prieurii*). I have not found any marked modification of contour at the base of the leaf in this family, and this coincides with the observations of PRANTL.*

This author describes the young leaf of *Trichomanes speciosum* (*l.c.*, p. 6) as having a two-sided apical cell, from which two longitudinal series of segments are cut off by converging walls. These segments divide by longitudinal walls, so as to form two series of cells, occupying the margins of the leaf (marginal series), and internal cells forming the central part of the leaf (compare PRANTL'S fig. 2, Taf. 1). Thus the phyllopodium is from the first, at least, *potentially* a flattened structure, which, by increase in bulk of the tissues derived from the internal cells and by continued growth at the margins, becomes a winged structure; the marginal series of cells are in a corresponding position to those which have been shown to be so intimately connected with the winged development in the leaves of other Ferns. As to the branching of the phyllopodium, it has been shown by PRANTL to be distinctly dichotomous, at least in the upper portions of the leaf; the upper part of the phyllopodium is thus a sympodial development. Further, it is clear that, the tissues of the leaf thus originating in the first place from a two-sided apical cell, and then from growth and repeated division of marginal series, of cells, are really the outcome of a development referable to a single plane, that is in two dimensions of space only.

Passing on to *Ceratopteris thalictroides*,† in which the development of the leaf has been so accurately followed by KNY, the apex of the young leaf is here also occupied by a two-sided apical cell, from which two series of segments are cut off; these segments divide, as in *Trichomanes*, in such a manner that a series of cells is formed running along each margin of the flattened leaf, and *continuous to its base* (compare KNY'S figs., Taf. 6); this character remains in the permanently angular cross-section of the lower part of the phyllopodium. Thus the leaf of *Ceratopteris* is also potentially a flat structure, which assumes a winged character by increase in bulk of the central part, and continued growth at the margins. The identity of the apical cell is subsequently lost, the apex of the leaf being then occupied by a continuation of the marginal series. The first pinnæ arise monopodially in acropetal order, and first appear as marginal outgrowths, but with no distinct reference to the segments of the apical cell. The structures which KNY calls stipular scales (stipular-schuppen), have a similar structure to the perulæ (spren-schuppen), and except in their position do not seem to me to be of a stipular nature.

The type of leaf-development seen in *Ceratopteris* prevails in its main characters also in other Ferns which have been investigated: *e.g.*, species of *Asplenium*,‡ in

* Unters. z. Morph. d. Gefässkrypt. Heft I. Leipzig, 1875.

† KNY, Die Entw. d. Parkeriaceen. Dresden, 1875.

‡ SADEBECK, Zur Wachsthumsges. d. Farrnwedels. Verh. d. bot. Ver. Brandenburg. Bd. 15 (1873), p. 123.

which SADEBECK followed the development; and as I have observed also in *Aspidium Filix-Mas*, *Polypodium vulgare*, and *Onoclea* (*Struthiopteris*) *germanica*, &c. The formation of the pinnæ in these cases is, at least at first, by monopodial branching, though it has been clearly shown that dichotomy may occur in the higher ramifications of the leaves of some Ferns.

Taking first *Aspidium Filix-Mas*, the marginal series of cells could not be distinctly traced as continuous to the extreme base of the phyllopodium in the young state, as is the case in *Ceratopteris*, and presumably also in *Trichomanes;* but such marginal series are clearly marked at the periphery of the pinnæ, and up to the extreme apex of the leaf. There is, however, a longitudinal weal on each side of the base of the phyllopodium, which is continuous upwards, with the usual winged development on the phyllopodium and the pinnæ, and it may easily be recognised in the mature leaf. This is doubtless the representative of, or a suppressed form of the wing-like development, which is, as in the cases before described, continuous to the base. In *Onoclea germanica* * the laterally widened basal part of the phyllopodium shows a similar external conformation to that in *Aspidium*, but the two marginal weals project more, and, as in *Aspidium*, may be easily recognised by their white colour. There is, however, no distinct development of wings in the usual sense of the term. Thus in the Ferns named, and they are merely taken as examples, the marginal developments may be traced to the base of the phyllopodium, and it may be concluded that this is a usual, if not a constant character for the Ferns. If this be so, the phyllopodium of the Ferns is typically a winged structure throughout its length, but in certain parts, and especially towards the base, the wings may be reduced, and only be recognised in the mature state as giving an angular form to the transverse section, or as light coloured, and very slightly projecting longitudinal ridges.

The *Hydropterideæ* are probably close allies of the other Leptosporangiate Ferns, but with their vegetative organs reduced in accordance with their aqueous habit. In this group there is a general reduction of development of the leaves, which, however, is apparent in different ways. Thus in *Azolla* there is a reduction of the phyllopodium to a minimum (if indeed the term may be applied at all), while the leaf has hardly any characters in common with the Fern-type. In *Salvinia* the early development of the leaves shows more points in common with the Fern-type, there being a two-sided apical cell, and, at least in the aërial leaves, a series of cells at each margin of the flattened leaf, similar in position and origin to that in the Ferns (compare Pringsh. Jahrb., Tom. 3, Taf. 25, fig. 7). In *Marsilia* the leaf is not of so reduced a type, and shows a clearly marked relation to the Fern-type. As shown by HANSTEIN,† there is at first

* This plant has been noted by GOEBEL (Bot. Ztg., 1880, p. 787) as an example of the occurrence of scale-leaves; some of the leaves lose their apical portion, which dries up, and is thrown off, while the basal part remains persistent. In the plant of *Onoclea*, which I had under observation, about half of the leaves had thrown off their apices in this way: the form of the basal portion which persists does not differ in any marked degree from the bases of the normally developed foliage leaves.

† Pringsh. Jahrb., Tom. 4, p. 245, &c.

a two-sided apical cell, the segments from which divide so as to produce two longitudinal, marginal series; these give rise at the apex of the phyllopodium to four pinnæ, which appear in acropetal order, and themselves have marginal series of cells as in the Ferns. The development of the leaf of *Pilularia* not having been thoroughly investigated, I have made a few observations upon it which show that it resembles that of *Marsilia.*

Pilularia globulifera.

The leaf of *Pilularia* has already been cited (p. 569) as an example of a simple phyllopodium, without appendages of any sort. It has been pointed out by AL. BRAUN * that it is connected with the Fern-type through *Marsilia,* in which the first formed leaves of the young seedling are without pinnæ.

In *Pilularia,* the conical, upturned apex of the horizontal axis bears members of three orders, which appear almost simultaneously in groups of three. They are, leaves which arise in two longitudinal rows on the dorsal † surface of the axis (Plate, 37, fig. 1, 1–7); buds, or lateral axes, one of which arises below each of the leaves, that is nearer the ventral side of the axis, and in the same transverse plane (fig. 1, *b*); and thirdly, roots formed endogenously, and similar in structure to those in *Marsilia.* One root is situated immediately below each bud (fig. 1, *r*).

The leaf appears first as an outgrowth of a single cell of the axis; in this cell divisions follow in regular succession cutting off two rows of segments from a two-sided, wedge-shaped, apical cell (figs. 2, 3). The position of the apical cell relatively to the axis appears, after the earliest stages, to be oblique, as seen in fig. 2. The further subdivision of the segments proceeds on the same plan as has been shown by HANSTEIN to obtain for *Marsilia.* The leaf assumes the circinate curvature at an early stage (fig. 1), and, as in other cases among the Filicineæ, it is not coiled accurately in one plane. The activity of the apical cell is continued until the process of extension of the lower portion of the leaf, and the consequent unrolling of the young leaf begins. No clearly marked region of intercalary growth is to be found; the process of extension is carried on uniformly throughout the tissues, beginning at the base and extending upwards. There is no continuation of the apical growth after the identity of the apical cell is lost, such as is found in the leaves of Ferns. Finally, the leaf develops from the first in a cylindrical form, and there is no prominent ridge to be found, nor any marginal series of cells similar to those in the Ferns and *Marsilia.* The cylindrical form is maintained to the extreme base. This leaf may thus be regarded as the simplest form of a phyllopodium, in which the mode of development is uniform from base to apex, and which bears no appendages. Though there is not any apparent

* Neuere Unters. über d. Gatt. Marsilia u. Pilularia.

† In speaking of horizontally growing axes, I use the term dorsal to signify the upper, and ventral the lower surfaces. In speaking of leaves, the term ventral is applied to the surface facing the axis, and dorsal to that which is turned away from the axis. This use of the terms is, however, obviously inconsistent, though it is now generally adopted.

formation of wings, still in the arrangement of the cells in the young leaf, and in their subdivisions, there are points in common with *Marsilia.*

Osmundaceæ.

I.—*Osmunda regalis*, L.

The young phyllopodium, before any pinnæ are formed, consists of an elongated basal portion with massive lateral wings, and a less distinctly winged apical portion, which is terminated by a bluntly conical, and comparatively massive apex: the whole is covered by numerous mucilaginous hairs. On removing the extreme apex by a transverse cut, and treating with suitable reagents, it is found that the apex is occupied by a *three-sided, conical, apical cell,* which is so situated that one side faces the apex of the stem, while the opposite angle is directed away from the apex of the stem, that is towards the dorsal side of the leaf (Plate 37, fig. 4). From this cell segments are cut off parallel to the three sides, in regular left-handed spiral* succession, as at the apex of the stem of *Equisetum.* The segments are further divided up fundamentally on the same plan as laid down by Cramer for *Equisetum,* and shown in the well-known figures copied in Sach's Text Book. Irregularities of arrangement of the walls are however to be found, as shown in the lower left-hand corner of fig. 4, on Plate 37. The apical cell remains clearly marked even after the first pinnæ have appeared: for instance, it was still to be seen at the apex of a leaf, which had already formed six pinnæ (Plate 37, fig. 5); but in one which had formed twelve pinnæ no apical cell was to be seen, while in the latter case the whole bulk of the conical apex was much smaller than in leaves at an earlier stage. After the three-sided apical cell has lost its identity, and the whole apex of the leaf has been reduced in bulk as above described, a marginal series of cells similar to, though less marked than in the case of other Ferns, is found extending over the apex of the leaf; but it has not been possible to recognise among the cells of this series any single cell acting the part of a two-sided apical cell.

The pinnæ are formed monopodially, and in strictly acropetal order on the phyllopodium: as in many Ferns, their insertion is not perfectly lateral, but towards the ventral face of the leaf, and along the lines of the more or less developed wings. The pinnules also appear in acropetal order, and are developed monopodially on the pinnæ. I have not seen any case of dichotomous branching in the leaf of *Osmunda regalis,* such as is described by Sadebeck, Prantl, and others as occurring in the leaf-branchings of higher order in many Leptosporangiate Ferns. It has been ascertained in the case of certain other Ferns that there is a distinct genetical relation between the pinnæ and the segments of the apical cell, though that relation is not

* *i.e.*, left-handed in the mechanical sense: the succession was left-handed in all the cases observed.

so close as was at first assumed by SADEBECK.* In these cases the two rows of pinnæ correspond to the two rows of segments of the two-sided apical cell, though the individual pinnæ have been shown by KNY not to correspond to the individual segments. It was thus suggested that a similar relation might be found in *Osmunda.* I have, however, been unable to discover any regular relation between the segments cut off from the apical cell and the individual pinnæ: the position of the latter is such that they must arise partly from the tissues derived from the ventral series of segments, partly from those derived from the lateral segments (Plate 37, fig. 5). This conclusion may be put in relation with KNY's observations on *Ceratopteris,* from which he finds that the pinnæ do not necessarily coincide with the segments of the apical cell: in *Osmunda,* however, the absence of such coincidence applies not only to the cells of one marginal series of segments, but also to the series of segments themselves.

The lower pinnæ appear in their early stages of development as rounded masses of tissue, in which no marginal series of cells can be recognised even when the pinnæ are viewed as in Plate 37, fig. 5. There is, it is true, a prevalence of cell-divisions in a direction perpendicular to the plane of the leaf over those parallel to that plane, but the distinction is not so complete as to mark off any marginal series. In the apical portions of pinnæ in later stages of development, as well as in the apical portion of the phyllopodium when further advanced, and in the later developed pinnæ, a marginal series may be recognised; in no case, however, is the marginal series so regular or so clearly marked as, for instance, in *Aspidium Filix-Mas* or *Ceratopteris thalictroides.* Thus, in *Osmunda regalis* the same mode of development by a marginal series of cells referable to a single plane is to be found as is prevalent throughout the leaf of the simpler Ferns. But in *Osmunda* it is relegated to the later stages only, viz.: at the apex of the phyllopodium and of the pinnæ when they are far advanced, and also in the later-formed pinnæ and the pinnules.

It has often been described how the basal part of the leaf of *Osmunda regalis* is widened laterally so as to form a sheath, while in those leaves in which the upper portion is aborted and dried up, it is this wider basal portion which forms the scale-leaf first noted by PRANTL. This widening is due to a transverse growth, chiefly in the peripheral tissues, including the superficial cells, the latter dividing repeatedly by periclinal walls. This growth in a transverse direction is most active at the lateral margins, that is at the points where a slight similar growth is found in other Ferns, *e.g.*, in *Onoclea germanica* and *Aspidium Filix-Mas*: or where in other Ferns there are well developed lateral wings, similar to those in the upper parts of the leaf. There can thus, after comparing *Osmunda* with other Ferns, be no doubt that the massive lateral wings at the base of the leaf are homologous with the similar, but less massively developed wings at corresponding points in other Ferns. Moreover the massive wings at the base of the leaf in *Osmunda* may be traced as continuous in the young leaf from

* SADEBECK, Verh. d. bot. Vereines. Prov. Brandenburg. Bd. 15, p. 129. KNY, Die Entw. d. Parkeriaceen, p. 40.

the base to the upper regions of the leaf, where they are interrupted by the insertions of the pinnæ. Thus the phyllopodium of *Osmunda* is a winged structure throughout its length, though the mode of the development of the wings is different at different parts of it, being more massive near the base, thus forming the sheath, and being less bulky, though still traceable, in the upper part.

Osmunda cinnamomea, L.

In this species also, a three-sided, conical, apical cell was found at the apex of the phyllopodium, and having a similar orientation to that in *O. regalis*. It may still be recognised after a considerable number of pinnæ have been formed. In all important points the leaf of this plant corresponds to that of *O. regalis* (Plate 37, fig. 6). In a leaf which had not yet formed any pinnæ, I was able to see clearly the relation of the massive wings at the base of the leaf to the apical cell; the limits between the rows of the segments could be traced as zig-zag lines down to the wings, thus showing that they are derived partly from the ventral, partly from the lateral segments (Plate 37, fig. 6).

In this species also the apical part of certain of the leaves becomes abortive, the basal part remaining as a permanent scale, as described by PRANTL for *O. regalis*.

Todea superba.

It was in this plant that the three-sided apical cell in the leaf was first found : since the *Osmundaceæ* differ from the other Leptosporangiate Ferns in various characters both external and anatomical, it was thought that an examination of the development of the leaf might bring interesting facts to light. The three-sided apical cell has the same orientation as in the two species of *Osmunda* described above, but its position does not appear to be maintained so exactly as in these plants, nor are the walls of segmentation so accurately parallel to the sides of the apical cell. Further, the subdivisions of the segments present more frequent irregularities (Plate 37, fig. 7). In the absence of distinct marginal series of cells in the early stages of the first formed pinnæ, and in the phyllopodium itself, while such marginal series are to be found in the later formed pinnæ, and in later stages of the earlier formed pinnæ, *Todea superba* corresponds to the above species of *Osmunda*. A peculiarity of structure of the wings on the higher ramifications of the leaf in this species cannot be passed over without remark. Transverse sections of the wings in these parts show that they consist of two, or at the margin of but one layer of cells; the corresponding parts of *T. barbara* consist of about nine layers. Thus between the species of a single genus, the affinity of which is indubitable, a very marked difference may exist in the bulk of the winged developments, and this should be borne in mind in considering the similar and simple structures in the Hymenophyllaceæ.

Attention must be paid to the basal portion of the leaf of *Todea superba*. Here, as

in *Osmunda,* there is on each side a massive winged development, which owes its origin to an activity of growth and division of the peripheral cells, including those at the surface. At first this development is, as in *Osmunda regalis* and *cinnamomea,* restricted to the lateral margins, and as in those plants, no doubt homologous with the basal winged development in other Ferns so often referred to (Plate 37, fig. 8, *a, b*). Later, however, the activity of growth and cell-division extends transversely across the face of the phyllopodium, and the result is a continuity of the transverse portion of the sheath with the lateral wings (Plate 37, fig. 8, *c*). In the mature leaf this may be clearly seen with the naked eye. This continuation of the winged structure across the face of the phyllopodium is comparable with that resulting in the so-called "axillary stipule," or with that which produces the familiar orbicular leaves, for example in *Tropæolum, Hydrocharis,* &c. (GOEBEL, Verlg. Entw., pp. 232–4). This case of *Todea* has an important bearing upon similar structures in *Angiopteris, Stangeria,* and *Ceratozamia.*

Todea superba appears to have no scale-leaves, with abortive apices, as in *Osmunda,* but in *Todea barbara* scale-leaves may be found in considerable numbers.

Comparing the development of the leaf in the *Osmundaceæ,* as shown in the above examples, with that of other Leptosporangiate Ferns, it is clear that an advance has been made in robustness of character of the phyllopodium, and therefore in its adaptation to serve as a supporting organ. As I have above pointed out, the growth with a two-sided apical cell, from the segments of which two marginal series of cells are derived, is to be looked upon in the case of the Fern leaf as a reminiscence of a development as a flattened expansion. This flattened expansion, by habitual thickening of the central portion, and frequently by corresponding reduction of the lateral wings, especially in the lower parts of the leaf, may be regarded as having given rise to structures such as the leaves of most Ferns. In the *Osmundaceæ,* though the winged character is not lost, the development of the apex of the leaf is of a massive and solid character from the first, and continues so as long as the apical cell persists ; it is a structure developed from the first, not in two, but in three dimensions of space. It has been clearly shown by the observations of TREUB on the apex of the stem of *Selaginella Martensii** that there is in that plant sometimes a two-sided, sometimes a three-sided apical cell, and that intermediate forms may be found between them : it might therefore be concluded that no great importance is necessarily to be attached to a difference in that respect. But in this case of the leaf in the Leptosporangiate Ferns the change from a two-sided to a three-sided cell is accompanied by changes of other characters, such as a more massive apex of the young leaf, the absence of marginal series of cells in the lower parts of the phyllopodium and pinnæ, as well as differences of internal structure, and in the reproductive organs. On these grounds it appears justifiable to attach more importance to this transition from the two-sided to the three-sided apical cell, than is necessarily implied by such a change. The leaf

* Recherches sur les organes de la végétation du Selaginella Martensii. SPRING. Leide, 1877.

in the *Osmundaceæ* may therefore be regarded as an advance upon the leaves of other Leptosporangiate Ferns; the phyllopodium is, at least in the part derived from the three-sided apical cell, a structure which develops from the first as a solid structure.

On the other hand, it is of interest to note that though there is this difference between the *Osmundaceæ* and other Leptosporangiate Ferns, still the conformation of the leaf is fundamentally the same. The phyllopodium and pinnæ, &c., are essentially winged structures to their extreme base. Putting this fact into relation with the observations of KNY, on the want of coincidence of origin of the pinnæ with the limits of the segments cut off from the apical cell in the leaf of *Ceratopteris*, and with TREUB's observations on *Selaginella Martensii*, it appears that the external conformation of the member or system of members is to a great extent independent of the arrangement of the internal cell-walls.

MARATTIACEÆ.

Angiopteris evecta, HOFFM., var. *pruinosa*, KUNTZE.

For comparison with the *Osmundaceæ* on the one hand, and with the *Cycadaceæ* on the other, I have had the opportunity of dissecting a well-grown plant of *Angiopteris evecta*, from Java. The amount of material being limited, several points of considerable interest have escaped observation, while on other points the evidence is not conclusive. This is especially the case with the observations on the apex of the stem. HOLLE remarks (Bot. Zeit., 1876, p. 218) that the reference of the cells of the *punctum vegetationis* to the divisions of a single apical cell is not certain, but he regards it as probable that they all originate thus from a single cell. My own observations point clearly to the existence of a wedge-shaped apical cell, but I am not in a position to state whether the cell has two or three edges, or what is the succession of segments cut off from it. Such a cell is represented in Plate 37, fig. 9, and though I will not vouch for the accuracy of direction of some of the less important cell-walls there drawn, this at least is quite secure, that the apical cell is a conical one, and that the tissues of the *punctum vegetationis* owe their origin to segments cut off from it. The question is left open whether this structure, found in a well-grown plant, is constant for the species.

The leaf originates as a flattened swelling of the surface of the very slightly conical apex of the stem. The growth is from the first more active on the side further removed from the apex of the stem (dorsal). The apex of the leaf is thus curved at an early stage towards the apex of the stem. A transverse semi-circular weal arises on the ventral side of the young leaf, and at some distance below the apex (Plate 37, figs. 10, 11); it soon shows signs of greater enlargement in its lateral portions than at the centre: this weal is the first origin of the well-known "stipules." The lateral portions grow rapidly, and overarch the more slowly growing, circinate apex of the leaf, in the manner already well known.

Holle states (*l.c.*, p. 218), I presume generally for *Marattia* and *Angiopteris*, though this is not made clear, that there is one wedge-shaped, pointed, apical cell at the apex of the young leaf, and that it may be found till after the appearance of the pinnæ. He describes it as being neither two-edged nor three-sided, but of irregular transverse section, while its divisions appear without definite regularity. I have satisfied myself, by observation both of medial longitudinal sections of leaves of various stages of development, and of transverse sections of the extreme apex of the leaf, that there is no such wedge-shaped cell at the apex of the leaf of *Angiopteris evecta:* a result which coincides with Holle's description, viz.: that there was irregularity of form and of succession of segments of the apical cell which he saw. Preparations were made by me from leaves varying in their state of development from the condition of a flattened papilla, to the period of formation of the pinnæ, and the same result was obtained from all, viz.: that there is not any single, conical, apical cell in the ordinary sense of the words.

My own observations show that the structure of the apex of the leaf of *Angiopteris evecta* is as follows. There are at the extreme apex a number of cells, larger than those surrounding them : as may be seen in median longitudial section, they are limited below by periclinal walls (Plate 37, fig. 12), and are thus clearly not wedge-shaped or conical cells. The cells of the apical region may be referred, in some cases at least, to a group of four initial cells (marked x in figs. 12 and 14), but these cannot always be equally well distinguished, and as seen in surface view from without, they exceed the surrounding cells but little, if at all, in size (figs. 13 and 14). These cells may be more clearly recognised when seen in a median longitudinal section of the apex of the leaf, in which case, of course, but two of them will appear. In such sections (fig. 12) the two cells appear separated from one another by a wall, which may be traced back continuously into the lower tissues of the leaf: they present an oblong outline, and exceed the average of the surrounding cells in depth. Passing away from the apical cell in either direction, the cells are seen to be smaller in average size : the prevailing mode of division is by successive periclinal and anticlinal walls, though, as may be seen in fig. 12, the succession of these is not strictly according to rule. A similar absence of regularity in the arrangement of the anticlinal walls may be seen in the figs. 13 and 14, which represent the apices of the leaves as seen from without. It is thus apparent that the arrangement of cells at the apex of the leaf of *Angiopteris* is similar to that described for the apex of the root.*

As the phyllopodium elongates, the pinnæ make their appearance on the ventral surface of it, and above the level of insertion of the stipules. All the evidence at my disposal points to a development of the pinnæ by monopodial branching of the phyllopodium in strictly acropetal succession, and in somewhat regular alternation on the two sides. They appear first as broad projections of the ventral face of the phyllopodium, and are arranged in two longitudinal rows, as in other Ferns (Plate 38,

* Russow, Vergl. Unters., p. 107. Schwendener, Bot. Ztg., 1880, p. 718.

fig. 15). They are at first similar in every external aspect to the pinnæ of *Cycas* of like age. Examination of the apices of the pinnæ showed that there is no single apical cell, nor are there, at least in early stages of development, any marginal series of cells, like those described for the leaves of the Leptosporangiate Ferns. The number of pinnæ formed is small as compared with the latter, and the phyllopodium, at least in some cases if not in all, terminates abruptly in a blunt cone, or terminal spine, such as is found so frequently among the *Cycadaceæ* (figs. 16 and 17).* This abrupt ending of the phyllopodium may sometimes be still recognised in the mature leaf, but it is usually obliterated by the more rapid growth of the parts immediately below it. When the succession of the pinnæ is clearly alternate, an appearance is then produced as though the development of the leaf were sympodial, and the last lateral pinnæ might be mistaken for the apex of the phyllopodium: observations of the development show however that this is not the case.

The pinnæ themselves assume the circinate curvature at an early stage (Plate 38, fig. 16): as their development proceeds they may either become themselves winged, as is the case in young or weak buds; or they may form pinnules, which also arise alternately, and in acropetal order, and are formed monopodially. Towards the apices of those pinnæ which form pinnules, a similar appearance as of a sympodial development is often found, and it may be explained as in the case of the phyllopodium. It is well known how frequently transitional forms are found between the winged development of pinnæ, and pinnules, and even higher forms of ramification, the latter being assumed by stronger plants: the result is a great irregularity of outline of the whole leaf.

The phyllopodium itself is but slightly winged, if at all: above the stipules it appears almost cylindrical, but in the upper parts of it traces may often be found of longitudinal markings where the wings would normally be situated, but the winged development is chiefly relegated to the branchings of higher order. When a winged development of a pinnæ or pinnule begins, the central mass of tissue of the member is already beginning to pass over to the condition of permanent tissue: active meristematic division is still continued at those peripheral points where the wings arise. Here the cells are arranged somewhat after the manner of the Leptosporangiate Ferns; but whereas in these the marginal cells constitute a simple linear series, in *Angiopteris* the structure is much more complicated; it is as though each cell of the marginal series of a leaf of one of the simpler Ferns were divided up by a number of anticlinal walls into cells of small and uniform size, arranged in regular series extending from the lower to the upper surface of the pinna or pinnule. Thus a transverse section would follow one of these series, as represented in Plate 38, fig. 19, in which may be seen in place of a single marginal cell, such as is seen in the transverse section

* In some examples of *Marattia* the phyllopodium is not thus abruptly terminated, but it is continued as an elongated, winged structure; the same is the case in *Danœa*.

of a leaf or pinna of a Leptosporangiate Fern,* a number of cells dividing by periclinal and anticlinal walls. Thus the correspondence of structure with that of the Leptosporangiate Ferns may be clearly seen, though the whole is much more complicated.

It will now be useful to compare the structure and development of the leaf of *Angiopteris evecta* as above described with that of the Leptosporangiate Ferns, and to note where the differences lie. It would be difficult to draw a comparison between the stipules of *Angiopteris* and any corresponding structure in the Ferns, were it not for the extension of the winged structure in *Todea* transversely across the face of the phyllopodium, so as to form the so-called "axillary stipule." As it is, however, this structure leads on as an obvious step to the stipular development in *Angiopteris:* the chief points of difference between them are (1) that the transverse portion of the structure appears in *Angiopteris in the first instance,* whereas in *Todea* it is of comparatively late origin; (2) that owing to the extreme shortness of the young phyllopodium in *Angiopteris* the longitudinal development of the basal wings is almost obliterated, while in *Todea,* and more clearly in *Osmunda,* it is very obvious, and may be traced upwards as continuous with the wings of the phyllopodium. By means of these intermediate forms supplied by the *Osmundaceæ,* we are, I think, justified in the conclusion that the peculiar stipular structures of the *Marattiaceæ* are merely modifications of the winged development at the base of the leaf.

In the arrangement of the meristem at the apex of the leaf of *Angiopteris* a decided advance is seen on that in the *Osmundaceæ,* and still more on that in the other Leptosporangiate Ferns. It was pointed out in the case of the leaf of the *Osmundaceæ* that the phyllopodium is, at least in the lower part where the three-sided cell was active, a structure which developed theoretically as well as practically in three dimensions of space. The same is the case in *Angiopteris* throughout the phyllopodium, in those cases at all events where it terminates abruptly. Further, the arrangement of the cells at the extreme apex is such, that the tissues cannot have been wholly derived from a single apical cell; there appears, on the contrary, to be a group of four apical cells: this is again a characteristic of a higher development, and it may be stated that in the arrangement of the meristem of the leaf, as also of the root, *Angiopteris* occupies an intermediate position between the Ferns and the plants of higher organisation.

The pinnæ and pinnules are here formed by monopodial branching; no case of dichotomy has been observed. They arise as rounded masses of tissue, not as flattened structures. The wings which are developed upon them are not referable to a simple linear series of cells, but appear as a massive weal on each side of the pinnæ or pinnule. In these points *Angiopteris* approaches the *Cycadaceæ* (*cf.* infra) rather than the Ferns.

Again, the pinnæ are comparatively few, and in some cases, if not in all, the

* KNY, *l.c.*, taf. 7, fig. 7, M. PRANTL, Hymenophyllaceen, taf. 3, figs. 38-54.

phyllopodium terminates abruptly in a blunt spine. This I have never observed among the Leptosporangiate Ferns: there it grows on, and becomes attenuated and flattened, thus apparently returning to its more primitive condition. All these characters, together with the almost entire absence of winged developments upon it, point to the conclusion that the phyllopodium in *Angiopteris* has assumed a more independent position than in other Ferns, and appears rather as a structure fitted to bear flattened assimilating organs, than as a flattened assimilating organ itself: we may compare this gradual self-assertion of the phyllopodium as a supporting organ, with what has no doubt taken place in the differentiation of axis and leaf, and say that the phyllopodium in *Angiopteris* betrays its *axial* nature more clearly than is the case in the less highly organised Ferns.

CYCADACEÆ.

Cycas Seemanni (ADOLPH BRAUN).

a. The Cotyledons.

Observations on the development of the leaf in the *Cycadaceæ* were begun on seeds and seedlings of *Cycas Seemanni* from Fiji: the seeds showed on dissection a bulky embryo, embedded in a massive endosperm (Plate 38, fig. 20). The embryo itself before germination consists of two long, almost equal cotyledons, inserted on a very short axis, which bears at its apex a number of young leaves in various stages of development. The cotyledons are not exactly alike; one is often larger than the other, while the margins of one usually overlap those of the other (Plate 38, fig. 21). It is not always the larger cotyledon which overlaps the other, though it may be presumed that it is the older one. Externally no trace of pinnæ has been found at the apices of the cotyledons, such as is shown in SCHACHT's drawing of *Zamia spiralis* (SACHS's Text Book, 2nd Engl. Ed., p. 501).

Transverse sections of the cotyledons show that there is sometimes a median bundle; in other cases no single bundle occupies a median position, but two equal bundles are disposed symmetrically near the centre of the cross section: intermediate modes of arrangement may be found between these two extremes. It might be assumed that the median bundle when present is merely the result of the coalescence of two equal bundles, which might be found to be distinct in the upper part of the cotyledon; but this is not the case, since the median bundle has been found to maintain its individuality in an upward direction. There is thus some irregularity in the arrangement of the vascular system in the cotyledons of *Cycas Seemanni*, though in the later formed leaves of this plant there is, as in the other *Cycadaceæ*, a constant absence of a single median bundle.* The development of the cotyledons has not been traced, since all the seeds at my disposal had mature embryos.

* Compare the description by DE BARY (Vergl. Anat. p. 246) of the vascular system in the cotyledons of Phaseolus, &c.; also my own observations and those of STRASBURGER on vascular bundles in the leaves of different species of *Gnetum* (infra, p. 599).

b. Plumular-leaves.

The first-formed plumular leaves are arranged in pairs, the first pair decussating with the cotyledons. As the plant grows older the arrangement of the subsequently-formed leaves is spiral.

The apex of the stem terminates in a flattened cone, in which, as described by STRASBURGER for *Cycas revoluta*, there is no single apical cell, but the cells at the periphery divide frequently by periclinal walls : there is thus no continuous layer of dermatogen covering the *punctum vegetationis*. The leaf makes its first appearance at the periphery of this flattened cone, as a simple, uniformly meristematic, hemispherical swelling, but with the side facing the apex of the stem slightly flattened. It is covered externally by a well marked and continuous layer of dermatogen : thus the above mentioned periclinal divisions of the peripheral cells are limited to the apex of the stem, and are not found in the young leaf. The growth of the leaf is not uniform in all directions, but is symmetrical on either side of the median plane : a slight hyponastic curvature of the phyllopodium is all that represents the circinate vernation of that part in the Ferns : this is more marked in old than in young plants (Plate 38, figs. 22, 23), thus the leaves of older plants overarch the apex more completely than is the case in younger plants. Growth is at first in a longitudinal direction, the cells dividing chiefly by transverse walls. The tissues of the young leaf, as seen in longitudinal section, are actively meristematic throughout, while the cells at the extreme apex show the relatively large nuclei, and thin walls characteristic of an apical meristem. Single cells of the dermatogen grow out as unicellular hairs, which are particularly numerous on the dorsal surface, and on the median portion of the ventral surface. These have to be removed in order to study the further development of the leaf, and are not, as a rule, represented in the figures.

While the whole leaf increases in length, transverse dilatation goes on unequally in different directions, and at different parts of its length. It is more marked in a direction perpendicular to the median plane than parallel to it, and though it is more extensive at the base of the leaf than it is higher up, still it is continuous throughout on the same plan. The result of this is that the leaf shows two marginal weals, which may be traced as continuous from the base to the apex (Plate 38, fig. 24). Starting from the base, it is found that the area of insertion of the leaf is semilunar, with somewhat rounded corners ; a transverse section of the leaf a little higher up shows a widening out of the corners as thin wings, and this increases upwards to a certain point, becoming then again gradually reduced. There is in fact a sheathing base to the young leaf of *Cycas*, which is produced by transverse dilatation throughout the tissues of the base of the leaf, but especially localised near the two margins (compare figs. 24 and 25). Tracing the marginal weals again upwards, they are found to extend uniformly as smooth, rounded, parallel ridges to the apex of the young leaf. The conformation of the whole phyllopodium from base to apex is fundamentally

uniform: speaking in a general sense, it is a *winged structure*, the wings being a subsequent development upon the more bulky central column (compare *Osmunda*).

In connexion with the further development of the leaf and the formation of the pinnæ, there are two questions to be decided: First, whether the pinnæ are formed monopodially or by dichotomy of the apex of the phyllopodium; and secondly, if they are formed monopodially, what is the order of their development?

In connexion with the former of these questions, it may be called to mind that a sympodial development of the leaf in the *Cycadaceæ* has been suggested by SACHS (Text Book, 2nd Engl. Edn., p. 503), on the ground of the conformation of the apex of the mature leaf: this idea is still maintained by some (FANKHAUSER; *Ginkgo biloba* p. 8, Bern, 1882), though the observations of WARMING ('Recherches et remarques sur les Cycadées,' Copenhague, 1877), which it must be confessed are not very complete, point to a monopodial development. My own observations show that in *Cycas Seemanni* (as also in all the *Cycadaceæ* in which I have had the opportunity of investigating this point) the development is *monopodial*. It is on the wings or ridges above described that pinnæ first make their appearance, and clearly below the extreme apex of the phyllopodium, which takes no direct part in their formation. There is first seen a slight undulation of the surface of the wings: this becomes gradually more pronounced, while the convexities gradually round themselves off, and finally appear as smooth hemispherical swellings. Still, though some of the pinnæ are formed by monopodial branching, there might be a gradual transition to a sympodial development of those formed later: a transition which probably does take place in many Ferns. This is naturally out of the question in those of the *Cycadaceæ*, to be described below, in which the order of succession of the pinnæ is exclusively basipetal. As to the remaining forms (*Cycas, Dioon*), the branching seems always to be monopodial, since the apex of the phyllopodium is throughout a much more bulky mass of tissue than the young pinnæ formed on it. It may therefore be concluded that the sympodial appearance of the apex of the mature leaf is misleading.

In approaching the second question, as to the order of succession of appearance of the pinnæ, it is obvious that their earliest stages of development should be observed; it is not sufficient to note the relative size of pinnæ, which have already passed the earliest stages; though such observations will give useful evidence, still they cannot be regarded as conclusive. In illustration of this I may quote an example, represented in Plate 38, fig. 26. In this case, passing from below upwards, pinnæ of various sizes are encountered, yet I have never had any direct evidence of irregularity in succession of formation of the pinnæ in any of the *Cycadaceæ*. Again, certain pinnæ may be arrested in their development at a comparatively early age (Plate 39, fig. 31); thus arguments drawn from any but the very earliest stages of development, though they may be admitted as secondary evidence, cannot be adopted for the ultimate decision of the question. Now, to judge from WARMING's drawings (*l.c.*, Taf. 3, figs. 19, 20), and from the description given by KARSTEN ('Organographische Betrachtung der *Zamia*

muricata,' p. 197), it is only comparatively late stages of development which have hitherto been observed. Hence, though the conclusions drawn are probably correct, they cannot be regarded as having been conclusively proved. (An exception may be made in the case of *Ceratozamia* observed by WARMING.)

In the case of young plants, such as the seedlings of *C. Seemanni,* there are practical difficulties in the way of a certain decision: thus the number of pinnæ on one leaf is comparatively small, while here, as in other cases among the *Cycadaceæ,* they arise almost simultaneously, and first appear as very slight undulations on the wings of the phyllopodium. Still, by comparison of a considerable number of cases, the conclusion has been arrived at that there are, in the case of *C. Seemanni,* distinct signs of a development of the pinnæ in *acropetal succession:* the pinnæ close to the apex, even in the youngest cases observed, are smaller than those lower down, while, in some instances at least, a similar diminution in size was observable in passing downwards towards the base of the leaf (Plates 38, 39, figs. 27, 28). These observations on leaves of young plants cannot be regarded as entirely satisfactory, but they acquire greater value when coupled with observations on an old plant of *C. Jenkinsiana,* to be detailed below, and with those of WARMING (*l.c.*) (*cf.* infra, p. 589).

The question remains whether there is any regular alternation in the appearance of the pinnæ on opposite sides of the phyllopodium. Some examples show that there is such an alternation, and this may be seen especially in the pinnæ nearest to the apex of the leaf. It was the prevalence of such alternation at the apex of the leaf of certain Cycads (*e.g.*, *C. revoluta*), which no doubt gave rise to the idea that the leaves develop sympodially. In other examples of *C. Seemanni,* no such alternation is to be found, and comparing the leaves, both young and mature, in a considerable number of cases, it is clearly seen that the arrangement of the pinnæ is neither constantly in opposite pairs nor regularly alternate on opposite sides of the leaf.

Finally, the position of the pinnæ at the apex of the mature leaf of *C. Seemanni* appears to illustrate the transition from the lateral to the terminal position. But, judging from young stages of development, I think it improbable that the apex of the phyllopodium, in this species at least, ever develops as a true winged structure; but rather that the apparently terminal pinna sometimes to be found is originally lateral, and gradually assumes the apparently terminal position as development proceeds. An accurately terminal pinna has never been observed in an early state of development, though one pinna may sometimes be nearer the apex than the rest, as in Plate 38, fig. 27. A comparison of a number of mature leaves of this species leads to the conclusions (1) that one apparently terminal or obliquely terminal pinna is about as frequent as two more or less exactly equal ones, and (2) that there is no apparent tendency for the older leaves to be more regular in this respect than the younger ones.

Up to the point of formation of the pinnæ, the development of all the leaves is alike, whether they appear when mature as foliage-leaves, or as the well-known scale-

leaves. But after the pinnæ have made their appearance, differences in the mode of development begin to be apparent, and make it necessary to treat of the two series of leaves separately.

c. *Foliage-leaves.*

The apical growth of the phyllopodium, which was never very marked, ceases with the appearance of the pinnæ; a slow intercalary growth is however maintained throughout its length, but is specially localised at different points in it at different times. In the basal portion the transverse intercalary growth is continued slowly throughout the transverse section, producing a widening of the sheath, which thus accommodates itself to the increasing bulk of the younger leaves within it; this transverse growth is accompanied by a slow longitudinal growth resulting in an elongation of the sheath. The most active intercalary growth goes on in the part of the phyllopodium above the sheath; this part elongates as the petiole, and carries the part which bears the pinnæ up with it. Meanwhile the pinnæ themselves remain in close juxtaposition one with another, the elongation of the part which bears them being subsequent to that of the lower part or petiole. From the observation of marks, originally drawn at equal distances apart on the young elongating leaf, it may be observed that the point of maximum activity of elongation is at first at some distance below the insertion of the pinnæ, and gradually proceeds upwards along the leaf; the final result is that the ultimate extension of the tissues is greatest in the sections immediately below the lowest pinnæ.

Meanwhile the petiole has increased in bulk, and presents the well-known almost cylindrical form, but the traces of the two longitudinal ridges may still be found in their original positions, and are well marked in certain other species (*e.g.*, *C. revoluta*).

Passing on now to the *pinnæ*, as above stated, these soon assume the form of rounded papillæ which show in section that they consist of a mass of meristem, covered by a well-marked dermatogen. These papillæ elongate transversely to the axis of the phyllopodium, but their growth is not specially localised, though there is a slight indication of this at the base of each pinna. The growth is unequal and hyponastic, resulting in the well-known circinate curvature of the young pinna. The tissues at the apex of the young pinna remain actively meristematic after two complete circles of circination have been completed, and even after the pinna has begun to uncurl; but the activity at or near that point is not greater than elsewhere. Soon after this the apex passes over to the condition of permanent tissue, and as it does not take part in the subsequent development of wings, it remains in the mature leaf as a distinctly acuminate process.

The rounded form of the young pinna is soon lost by the formation of lateral *wings* similar in relative position to those on the phyllopodium. A transverse section of a very young pinna shows an almost circular outline, while the tissues appear undifferentiated, and all the cells capable of division. Later the longitudinal divisions, *i.e.*, in planes parallel to the organic axis of the pinna, cease in the central portion of

the section, while the cells increase in size, the whole forming the *midrib* of the pinna. Cell-divisions are however continued below the epidermis at the dorsal side of the pinna, thus forming the *hypoderma* (KRAUS, Cycadeenfiedern, pp. 321–323); also along the ventral surface, and especially at the two angles of the section. Here the cell-division is particularly active both in the epidermis and the sub-adjacent tissues, and the arrangement of the walls is almost exclusively anticlinal, *i.e.*, in planes perpendicular to the external surface. Thus at the margins of the ventral face of the pinna, two *wings* are formed, which consist of a number of internal layers of cells, varying in number from 10 near the midrib to about 8 at the margin, and covered externally by the continuous layer of dermatogen. As is well known, a single vascular bundle traverses the midrib of each pinna longitudinally, to the apex; no lateral branches are given off from it. Accordingly there is no disturbance of the layers of cells in the wings by sub-division and formation of procambial bundles; instead of this the cells of the four or five central layers cease their anticlinal division, the cells elongate, and those nearest the centre form the *transfusion-tissue of Mohl.* The two layers, adjoining the upper and lower layers of epidermis respectively, develop irregularly; cells of the outer layer sometimes forming hypoderma (and this is especially the case at the margin); sometimes they develop as palisade parenchyma, especially at the upper surface. The layer immediately below it accommodates itself to the mode of development of the outer layer. The wings extend throughout the mature pinna from closely below the acuminate apex to the base, and on the side nearest the base of the leaf the wing is continued for a short distance down the phyllopodium.

d. Scale-leaves.

The first leaves which succeed the cotyledons develop only as scale-leaves, and leaves of similar form alternate with the later, more fully developed foliage-leaves. It has been above stated that in their first origin, and up to the time of appearance of the pinnæ, there is no perceptible difference between the scale- and foliage-leaves. The differences which appear later are as follows :—The pinnæ do not advance beyond a rudimentary stage, and remain as rounded papillæ; later the whole of the upper part of the leaf with the pinnæ becomes dried up (compare *Osmunda*, &c.). The lower sheathing portion of the scale-leaf differs in bulk from that of the foliage-leaf, the former being much less massive, while the curve described by the inner surface, as seen in transverse section, is much larger than in the latter (Plate 39, fig. 29, *a*, *b*). Differences may also be recognised in internal structure, though the plan on which the two forms of leaf are constructed is identical; thus the arrangement of the vascular bundles is closely similar in scale- and foliage-leaves, but while a band of sclerenchyma extends along both the upper and lower surfaces of the basal part of the foliage-leaf, that tissue is almost absent from the scale-leaf.

Thus, as has been pointed out by GOEBEL (Bot. Zeit., 1880, p. 784), but without

investigating them developmentally or anatomically, the scale-leaves are to be regarded simply as altered foliage leaves, which might have developed as such, but are arrested at an early stage ; their basal portion is proportionally widened, and their apical part aborted (compare *Onoclea, Osmunda,* and *Todea barbara*).

Cycas Jenkinsiana, GRIFF.

The above observations on seedlings of *Cycas Seemanni* not having been quite conclusive on the point of the order in which the pinnæ appear, it was desirable to control them by observations on some older plant, the leaves of which produce a large number of pinnæ. *Cycas Jenkinsiana* was selected for this purpose ; the individual plant bore on one leaf about forty pinnæ on each side, those on opposite sides being arranged in more or less regular pairs. In addition to these there were about ten pairs of spines on the lower part of the leaf, corresponding in position to the pinnæ, and, as will be shown below, produced in the same manner as the pinnæ with which they are homologous. The young leaf of this species is similar in general conformation to that in *C. Seemanni;* it consists of a central columnar portion, on which are formed two lateral, longitudinal ridges. These are most strongly developed at the base of the leaf, forming a more prominent sheath than in *C. Seemanni;* they may, however, be clearly traced as continuous to the apex of the leaf, which is thus in its early state a simple winged phyllopodium.

The numerous pinnæ make their appearance almost simultaneously throughout the entire length of the lateral wings, as gentle undulations, which gradually assume the form of rounded papillæ. There is a slight but unmistakable indication of a priority of appearance of those pinnæ which are formed about the middle of the leaf, while those nearer the apex and the base appear rather later (Plate 39, fig. 30). This observation thus corroborates that of WARMING (*l.c.*, Taf. 3, fig. 20), though the difference seems to be less marked here than in WARMING's specimen of *Cycas circinalis.* In the development of the normal pinnæ there is no difference from *C. Seemanni* requiring further remark ; but as may readily be seen at the lower part of the mature leaf, there is a gradual transition downwards from the normal pinnæ to reduced spinous structures, which occupy a position similar to the pinnæ, and are doubtless due to arrested development of homologous structures. This view is thoroughly borne out by observations of their development. It may be seen in leaves in which extension has not begun, that the formation of pinnæ is continued along the wings in a basipetal direction almost down to the sheath. It is just above the sheath that the petiolar extension begins, and it is most marked over the lower part of that region on which pinnæ have already appeared. These lower pinnæ are thus separated a considerable distance one from another (Plate 39, fig. 31), at the same time they remain in a comparatively rudimentary state, and do not keep pace with the increase in size of the pinnæ above the region

of early extension; this check, which the lower pinnæ suffer at this early period, is permanent, and they appear on the mature leaf as the spines above described.

It is clear that we have here a further example of a phenomenon noted long ago by A. DE ST. HILAIRE,* and called by him "balancement d'organes," and which has long been recognised by botanists. This mutual dependence of organs one upon another in respect of their individual development has been recently again described and experimented upon by GOEBEL (Bot. Zeit., 1880, p. 809, &c.), and designated "correlation of growth." This author has demonstrated that there is a mutual dependence in the mode and extent of their development, between the main shoot and lateral shoots, between the foliage- and scale-leaves of a single shoot, and further between the sporangia and the vegetative development of the shoot which bears them: a stronger development of the former structure in each of these cases being shown in a series of examples to be accompanied by a reduction of the latter, while if, artificially or naturally, the former structure be removed or reduced, at an early stage of development, that removal or reduction is followed by a correspondingly stronger development of the latter structures. He further pointed out that this correlation has a very wide influence upon the conformation of the members of plants.

In the leaf of *Cycas Jenkinsiana* the correlation may be followed a step further, and be recognised as prevailing between the parts of a single leaf. The pinnæ situated upon that part of the phyllopodium where growth and extension begin at an early period are arrested in their growth and develop as spines, while those borne by that part of the phyllopodium which extends only at a later period are not so arrested, but grow into normal, winged pinnæ. A similar correlation appears to me to afford at least a partial explanation of the very rudimentary condition of the winged structures on the petiole in Cycads, and in many Ferns. Probably a correlation such as this is very widely spread among plants, and especially in those with petiolate leaves. A more exact study of these, and especially of the distribution of their growth, not in space only, but also in time, would doubtless lead to an explanation of many familiar phenomena of *form.*

Dioon edule.

From the arrangement of parts at the apex of the leaf of *Dioon*, it appeared not improbable that that genus would approach *Cycas* more closely in the order of origin of the pinnæ than others of the *Encephalarteæ*. The plant on which observations were made bore one mature foliage-leaf, which had on each side about 50 pinnæ. Both scale- and foliage-leaves in *Dioon edule* have a comparatively narrow base, but immediately above the point of insertion the margin curves suddenly in a lateral direction, so that the basal portion of the leaf is broadly sheathing. The wings of this sheath may be traced upwards, as in the leaf of *Cycas*, to the apex of the phyllopodium. As in *Cycas* the pinnæ appear on those ridges, and in leaves in which they

* Leçons de Botanique, p. 226, 1840.

had already been formed in considerable numbers, it was clear that the development proceeded in a basipetal direction. This could be proved as follows, on the assumption that leaves formed subsequently to those already developed would form *approximately* as many pinnæ as they. The foliage-leaf of this plant of *Dioon* formed about 50 pinnæ on each side. In one young leaf, which showed no sign of apical growth, there were about 25 pinnæ on each side, while those nearer the base were successively smaller than those above, till their identity was gradually lost in the smooth ridge; a considerable space, however, intervened between the lowest traces of the undulation and the sheathing wings. These facts being so, and the next older leaf having a larger number of pinnæ, while the next younger one had fewer, the conclusion may be safely drawn that *there is a formation of pinnæ in basipetal order of succession.* But this does not exclude the possibility of a simultaneous development in an acropetal succession, at least among the earliest formed pinnæ, and the observation of younger leaves, in which the formation of pinnæ is just beginning, gives good evidence that there is also an acropetal succession, which is, however, soon arrested. Thus on the youngest leaf of the plant in question, which bore any traces of pinnæ, it was distinctly seen that those at the extreme apex of the leaf were smaller than those slightly lower, while those lower still were again smaller (Plate 39, fig. 32). This appearance not being supported by observations of more than a single specimen, is capable of two interpretations: (1) There may be, and I think that there almost certainly is, a weak acropetal succession, only a few pinnæ being formed subsequently to, and above those which first appear: to prove this is impossible on a single specimen, since the same difficulties arise here as in *Cycas Seemanni,* and *Stangeria,* and other cases where the number of pinnæ is small; (2) It may be that the development is really basipetal throughout, but that those pinnæ which are nearest to the apex develop less strongly than those formed below, but subsequently to them. I am unable to give a decided opinion either way, but think the former interpretation is by far the more probable. If it were distinctly proved, the case would be an interesting one for comparison with *Cycas,* since it would be the only example among those *Encephalarteæ* which I have investigated, of even a limited acropetal order of succession of the pinnæ; moreover, there would thus be added one more character in common between *Cycas* and *Dioon.*

Macrozamia Miqueli.

The material at my disposal consisted of young plants only. These showed on the mature leaf a terminal spine, representing the apex of the phyllopodium. It was never observed to have developed as a winged structure. On the phyllopodium are borne pinnæ, usually to the number (in the plants investigated) of about 16 on each side: those at the apex of the leaf are usually arranged in equal pairs, though they are sometimes irregular. The base of the phyllopodium is as usual developed as a

winged sheath. The pinnæ frequently have marginal teeth, which vary in number and size, not only from plant to plant, but also from leaf to leaf. While one plant observed had hardly any teeth on any of its pinnæ, most of them had several on each pinna, the number varying from two to four or five: thus the occurrence of these teeth is a very inconstant phenomenon.

Turning to the process of development, the young leaf of *M. Miqueli* has a similar form to that described for other Cycads (Plate 39, fig. 33), viz.: it is conical, with the ventral face flattened, and it is traversed from base to apex by two lateral ridges, which are extended near the base as sheathing wings. In their upper part, *i.e.*, above the wings, they are at first smooth; as the leaf grows older, undulations appear first close to the apex; these undulations, which are the first indications of the young pinnæ, round themselves off as hemispherical papillæ; later they assume an ellipsoidal form (Plate 39, figs. 34, 35). As to the order of succession in the appearance of the pinnæ it can be clearly proved in this plant that it is *basipetal*, the same arguments being applicable here as in *Dioon edule.* But there is this difference between the two, that whereas in *Dioon* there are traces of an acropetal order of succession in the pinnæ nearest the apex, such a succession is completely absent in *Macrozamia.* It will be obvious from a comparison of figs. 33 to 35 that though the leaf may at first increase in length by apical growth, this ceases soon after the formation of the first pinnæ, and the subsequent elongation must be intercalary: also it may be readily proved by measurements that this intercalary growth is more active in the lower part (*e.g.*, below the fifth highest pinnæ in the figs.) than in the upper part of the leaf: a similar observation will apply to other examples described below.

The basipetal succession is also maintained by the pinnæ in their further development: those situated near to the apex of the leaf are the first to assume the ellipsoidal form above mentioned (Plate 39, fig. 35): the longer axis of the ellipse is placed obliquely to the axis of the phyllopodium, the lower end of the axis pointing outwards: this corresponds to that oblique insertion of the pinnæ to be observed in the mature leaf of so many Cycads (Plate 39, fig. 37). Very soon after assuming the ellipsoidal form, the pinnæ show traces of a marginal crenation (Plate 39, figs. 35, 36), the number of lobes is small, and corresponds to the number of teeth of the pinnæ, of which they are the first indication: the teeth thus appear at a very early period, before the tissues of the pinnæ are differentiated, and a considerable time before the lignification of the elements of the xylem.

The pinnæ in their further development show a localisation of their intercalary growth below the teeth (or *pinnules,* as they may perhaps be called), so that in the mature pinna the teeth are situated at or very near to the apex. It has been impossible to find any single lobe *constantly* in advance of the others, which could in any sense be regarded as the apex of the pinna: still, one lobe is frequently more prominent than the rest (compare figs.).

Encephalartos Barteri.

This plant affords a most conclusive proof of a development of pinnæ *exclusively in basipetal order*. The average number of pinnæ on each side of the mature leaf of the plant investigated was rather over 40. The apex of the phyllopodium extends beyond the topmost pinnæ as a short terminal spine: at the margin of the mature pinnæ, and especially near the apex, a number of spinous outgrowths (pinnules ?) are formed.

The leaf has in its early stages of development a similar conformation to that in the forms already described, but the wings at the base of the leaf are of large size, and subsequently extend upwards as in *Ceratozamia* (*cf.* infra). No pinnæ are formed, at least in the plant dissected, till the young leaf has attained a considerable size, with well developed ridges running to the apex (Plate 39, fig. 38). The formation of pinnæ then begins close to the apex, as a series of rounded papillæ, which subsequently become ellipsoidal, their longer axes being oblique to the phyllopodium (Plate 39, fig. 39). There are no signs of any development of pinnæ in acropetal order; on the other hand all evidence tends to show that the order of succession is exclusively basipetal. Thus (1), the pinnæ decrease in size from above downwards; (2) as above mentioned, the average number of pinnæ on each side of the leaf of the plant in question was over 40: in the leaf represented in Plate 39, fig. 39, there are 12 on each side, while a considerable space intervenes between the lowest pinnæ and the basal wings; in the next older leaves this space is occupied by young pinnæ. There is thus conclusive proof of an *exclusively basipetal* order of development of the pinnæ in this plant. Marginal spines, similar to those in *Macrozamia Miqueli*, are formed at a comparatively early period on the pinnæ.

Ceratozamia Mexicana, Brong.

Observations were made upon a well-grown plant of this species, which had four fully-developed foliage-leaves. Each of these bore from 18 to 28 pinnæ, that is 9 to 14 on each side of the phyllopodium. The pinnæ near the apex are arranged in regular pairs, while those nearer the base are less regular in this respect; and it may be here remarked that this is generally, but by no means always, the case with those members of this group in which the development proceeds in basipetal order. On the other hand, in those plants which like *Cycas* have divaricating order of development, the pairs at the point where development first begins are most regular, while the regularity is not so marked in the later formed pinnæ. There appears then to be, roughly speaking, a tendency to regularity of arrangement in pairs among the pinnæ first formed, and a gradually increasing irregularity in those formed later. But this does not hold without exception.

The lower part of the phyllopodium, when mature, bears numerous spines irregularly arranged. These resemble the spine-like pinnæ of *C. Jenkinsiana* in

general appearance, but not in position. They were not to be found upon the young leaves of the plant investigated, and this would point to a late origin, which, together with the irregularity of their arrangement, would give them the rank of emergencies. This cannot, however, be accepted as conclusive, since they are entirely absent from some leaves, even when mature, and that may have been the case with the young leaves which were observed. However this may be, they are certainly not constant in occurrence nor in arrangement.

In very young leaves, before the pinnæ make their appearance, there are to be seen two lateral, basal wings, as represented by WARMING (*l.c.*, Taf. 4, figs. 16–19) for *Ceratozamia longifolia.* As in other cases these may be traced upwards in the young leaf, and be seen to be continuous with the two lateral ridges, which run to the apex of the phyllopodium. The phyllopodium is thus, as in other cases, fundamentally a winged structure. As the leaf grows older the basal wings become elongated upwards as broad flaps (*cf.* WARMING's figure, *l.c.*, Taf. 4, 19). Up to the time of appearance of the first pinnæ there is no connexion between the flaps transversely across the face of the phyllopodium. At a later period, after the pinnæ have begun to be formed, a more or less irregular and lobed extension of the wings is formed on the face of the phyllopodium, which connects the two wings one with another, and remains permanently, so that it can readily be recognised at the base of the mature foliage-leaf, and may be found also on the ventral face of the scale-leaf. This connexion between the wings transversely across the face of the phyllopodium is interesting when compared with other examples of a similar process above described: thus in *Todea* and in *Angiopteris* similar developments have been noted; but there is a difference in the *time* of development: thus in *Todea* and in *Ceratozamia* the connexion appears at a comparatively late period, whereas in *Angiopteris* the transverse connexion is present from the first.

As described by WARMING, the order of formation of the pinnæ is basipetal. This may be proved in the same way as in *Encephalartos Barteri* (Plate 40, fig. 40). The young pinnæ are much like those of *Zamia*, but the margin is not undulated, but smooth.

Zamia muricata.

As statements have already been made by KARSTEN * as to the development of the leaf in this plant, it was important to observe the early stages of the process carefully, and especially so because his observations do not coincide with my own and with WARMING's on *Macrozamia* and *Ceratozamia*, &c. From the passages quoted it appears

* Org. Betr. *d. Zamia muricata*, p. 197. He says: "Alle Fiederblättchen erscheinen bei ihrem ersten Auftreten in der Form halbmondförmiger Wülste;" and later on, p. 211: "Von mehr Bedeutung würde für den Vergleich der Cycadeen mit den Farren die Entwickelungsgeschichte und Entfaltungsweise der Blätter gewesen sein, die bei diesen Familien gleichmässig von unten nach oben fortschreitet, während bei den übrigen Phanerogamen die Entfaltung des Blattes von oben nach unten."

that he thought that at least in *Zamia muricata* the development of the whole leaf, and its extension proceeded from base to apex. In the former of the two passages however he describes the first appearance of the pinnæ as "semi-lunar weals"; this does not correspond to my own observations on other Cycads. Thus there are two questions to be decided: first, in what form do the pinnæ first appear? second, do they appear in acropetal or in basipetal succession?

On examining young leaves of *Zamia muricata* it was found that the form of the pinnæ on first appearance, and their order of succession, were similar in all essential points to that described in *Macrozamia* and *Ceratozamia.* Thus the pinnæ do not arise as "half-moon-shaped weals" but as undulations of the surface of the ridges, which round themselves off as hemispherical papillæ, and then subsequently assume the obliquely ellipsoidal form. Further, the order of succession of their appearance is clearly *basipetal,* and no signs of any acropetal succession were found in the leaves investigated. Judging from KARSTEN'S description of the first appearance of the pinnæ as "semi-lunar weals," I should think that he did not see the earliest stages of their development at all, though such observations alone can give true ground for statements as to the order of development of the parts of the leaf.

Marginal crenations or teeth are found on the pinnæ of most if not all species of *Zamia,* and some observations were made upon their origin, and the time of their appearance. They are absent from the basal part of the pinnæ; the margin of the apical part of the pinna is seen at an early stage to be crenated (*Z. Boliviana?* = *Loddegesii*), even while the lignification of the vascular bundles has hardly begun: as to the order of development of the crenations, I have not been able to come to any conclusion, but it may readily be seen in young pinnæ that they are more marked at the lateral margins than at the apex. Each crenation corresponds in position to the end of one of the procambial strands, or vascular bundles: this may be compared with what has already been observed by PRANTL* in the leaves of certain Ferns, in which, as he describes it, the ends of some of the nerves (hence called *ribs, costæ*) perform the function of growing points during the development of the leaf: a similar but very rudimentary development is to be found in most of the *Encephalarteæ,* also in *Botrychium,* and in *Ginkgo.*

The phyllopodium of *Zamia* ends in a terminal spine. During the extension and unfolding of the leaf there is a curvature of the phyllopodium, which has been regarded as bearing an outward resemblance to leaves with circinate vernation. This curvature, however, appears only at a comparatively late period, the phyllopodium of young leaves being straight in those plants both of *Zamia* and of *Ceratozamia,* which I have observed.

* Untersuchungen zur Morphologie der Gefässkryptogamen. Heft I., p. 4, &c., Heft II., p. 4, &c.

Stangeria paradoxa.

This genus of the *Cycadaceæ* approaches the *Marattiaceæ* more nearly in external aspect than the rest: the venation of the expanded pinnæ, their small number, and the sheathing stipule are common characters, which at once assert themselves. The superficial resemblance is so strong that the plant was first described as a Fern by KUNTZE.* It was thus a matter of considerable interest to work over the development of the leaf in *Stangeria paradoxa*, and to compare it on the one hand with *Angiopteris*, and on the other with the rest of the *Cycadaceæ*.

In the first place, the idea suggests itself that there might be a closer correspondence between this plant and *Angiopteris* in the characters of the apical meristem than is found in other *Cycadaceæ*. Sections showed that this is not the case, the apex neither of the stem nor of the leaf of *Stangeria* showing any greater similarity to those of *Angiopteris* than that of *Cycas*.

The leaves appear as broad roundish swellings on the conical apex. At a very early period an outgrowth of the ventral face appears below the apex of the young phyllopodium, and results in the formation of a transverse weal or ridge, which is curved downwards at the lateral margin, and thus presents a convex upper surface (Plate 40, figs. 41, 42). This *axillary stipule*, as it may be called according to the present terminology, grows to a considerable size, and overarches in the first place the apex of the stem, and also the successively formed younger leaves (Plate 40, fig. 44). When seen from above it may be observed that there is a slight median emargination, which however is not very pronounced at any period. This structure appears to be the homologue of the similar structures in *Angiopteris*, *Todea*, and *Ceratozamia*.

The part of the phyllopodium immediately above the sheath does not show clearly marked longitudinal weals (compare *Angiopteris* and *Todea*), though a winged structure is slightly apparent in the upper portions of the mature leaf in all the plants named which have this conformation at the base. Some time after the sheath is formed and considerably advanced, the pinnæ make their appearance. Their number being small, and the material limited, I have been unable to observe the order of their development with certainty. As in other Cycads, they appear when young as rounded papillæ, and are arranged in two longitudinal rows. There is some irregularity in the manner in which they are disposed at the apex of the phyllopodium. In some leaves there are two equal pinnæ placed symmetrically on either side of the apex (Plate 40, fig. 44), while the latter may be sometimes recognised at the back of them as a very minute projection.† In other cases there is a distinctly median pinna borne at the apex of the phyllopodium, or it may be that the apex of the phyllopodium itself grows on as an elongated winged structure,

* *Stangeria paradoxa*=*Lomaria coriacea*, *L. eriopus*. KUNTZE, Linn. x., 102, 506, and xviii., 116.

† Such an arrangement calls to mind that often found at the apex of the leaf of *Botrychium* or, as a still more reduced form of a similar arrangement, the apex of the leaf of *Ginkgo*.

similar to the pinnæ. The pinnæ elongate, but remain straight (Plate 40, fig. 45); at the margins of the ventral surface a winged development begins, which is continued here over the extreme apex of the pinna, thus producing that appearance of a gradual fading away of the midrib, towards the apex of the pinnæ.

Turning now to the details of development of the pinna, it is seen in transverse sections of pinnæ of various ages that at all times the external surface is covered by a continuous layer of dermatogen, in which periclinal cell-divisions never occur. At the very first appearance of the wings, both periclinal and anticlinal divisions are found in the cells lying below the dermatogen; but soon the former cease, and as the result of continued and successive anticlinal division, the wings as they develop are composed as in *Cycas* of a number of clearly-defined layers of cells, enclosed by the dermatogen: their number varies from about eight or more (exclusive of the dermatogen) at points close to the midrib, to six or five towards the margin. The regularity of these layers is subsequently disturbed by the occurrence of periclinal walls also, along the course of the future vascular bundles, thus resulting in the formation of procambial strands. About the same time as the procambial strands make their appearance the margins of the wings become gently serrated, especially near the apex: the serration is already clearly marked before lignification begins in the wings, but its appearance is subsequent to that of the lignification in the midrib. The chief increase in surface of the pinna is by intercalary, longitudinal and transverse growth. It is thus apparent that the development of the wings is closely similar to that in *Cycas*, or in *Gnetum* (infra); also that though the ultimate external appearance of the pinna resembles that of *Angiopteris* more than either of the above genera, still there is between the two this difference in their mode of development: that whereas there is a clearly marked and continuous dermatogen in *Stangeria*, in *Angiopteris* there are repeated and frequent periclinal divisions in the peripheral cells, and especially in those near the margin of the young wing.

GNETACEÆ.

Gnetum Gnemon.

Having already prepared notes on the development of the leaf in the *Gnetaceæ*, it appeared to me better to embody the results in the present paper along with those above detailed than to defer their publication; moreover this course is justified by the bearing which those results have upon the general subject now in hand.

The cotyledons of *Gnetum Gnemon* develop in a similar way to the ordinary foliage leaves. These arise in decussating pairs, and at first appear as rounded papillæ: the apices of these papillæ soon become slightly elongated, so that the form of the whole young leaf is acutely conical, while below it is massive (Plate 40, figs. 47–50). At first cell-division and concomitant growth go on almost uniformly throughout the young leaf, but even at such an early stage as that represented in Plate 40, fig. 47,

the cells of the internal tissue at the extreme apex of the leaf contain single, large, compound crystals apparently of calcium oxalate ; these remain permanently as the leaves develop, and point to an early cessation of meristematic activity in the tissues at the apex of the leaf. The tissues below this apex of the conical phyllopodium retain their activity and growth, which go on almost uniformly for a time over the whole of any given tranverse section. Soon, however, differences appear in this respect ; the cells of the dorsal side of the phyllopodium cease to divide in longitudinal planes, though longitudinal sections show that most of the elements continue to divide by tranverse walls : at the same time the dorsal portion increases in bulk, while the tissues become differentiated, and show all the signs of passing over to permanent tissue. Along the ventral surface of the leaf, however, and especially at the two corners of its outline of transverse section, which is now angular, the cells still divide in longitudinal planes, and show signs of great meristematic activity : the division-walls, which appear at the corners of the section, show considerable regularity of arrangement. All those divisions of this period which can be seen in a transverse section are anticlinal: the result of this, together with the accompanying growth, is the formation of two projecting wings attached at the corners of the ventral side of the phyllopodium (Plate 40, figs. 49, 50), and extending from close below the apex, which is itself not winged, almost to the base. Since all the divisions of cells in the wings are at first anticlinal, the tissues develop as well-defined layers, parallel to the outer surfaces ; each wing consists of upper and lower layers of dermatogen, which, as usual, cover the surface externally, and enclose eight or nine regularly arranged layers of internal tissue. The growth of the wings is not localised at any definite point, but the divisions at the margin are less frequent than nearer the midrib : this shows that the growth is intercalary, not marginal, as in the Ferns. The uniformity of arrangement of the divisions in the wings is disturbed at certain points by the appearance of periclinal and irregular divisions in the central layers, which result in the formation of procambial strands. The periclinal divisions also extend in some cases, where a large bundle is formed, to the layers immediately below the dermatogen ; the cells thus produced, together with the vascular bundle which they enclose, form one of those ribs which project on the lower surface of the mature wing.

Applying the same terminology as has been used above, it is obvious that the leaf of *Gnetum Gnemon* is a simple unbranched phyllopodium, on which wings are developed in a corresponding position to those in the Ferns and Cycads : there is no definite peculiarity of conformation at the base of the phyllopodium, beyond a slight increase in bulk towards the base, which assumes the form of a smooth transverse ridge on the ventral face, above the position of those glandular structures which I have described elsewhere (Quart. Journ. Micr. Sci., vol. xxii., p. 283, plate 35, fig. 19). The wings themselves develop in a manner very similar to those of the pinnæ of *Cycas* or *Stangeria*, until the special peculiarities accompanying the formation of the vascular bundles and ribs make their appearance. Comparing the leaf of *Gnetum*

with that of the Cycadaceæ it appears that the two structures are not unlike at an early period (figs. 49, 38, 33, 24); the difference between them when mature depends mainly upon the large development of the pinnæ, and the almost complete abortion of the wings of the phyllopodium in the Cycadaceæ, while in *Gnetum* the pinnæ are entirely absent, and are replaced by a larger development of the wings.

A few words must be said upon a certain irregularity in the arrangement of the bundle-system in species of *Gnetum*, though this lies outside the present subject. As already described (*l.c.*, p. 285), the leaf-trace of *Gnetum Gnemon* consists of five bundles, one being median. I have found the number of bundles of the leaf-trace to be uneven, one bundle being median, in the following specimens supplied from the Herbarium at Kew: *G. latifolium*, Celebes; *G. paniculatum*, Brazil; *G. scandens*, *G. venosum*, America; also in an unnamed species (MOTLEY, No. 1063) from Borneo. In these plants the single median bundle could be traced as continuous from the stem into the upper regions of the leaf, and it coalesces with the lateral bundles rarely, if at all. In one species, viz., *G. Africanum*,* the central bundle is found to be absent: the leaf-trace consists here of but four bundles disposed in two pairs. Tracing these upwards into the leaf, they are found to take distinct courses, and in the leaf which I investigated, no fusion was seen to take place between the pairs. This difference of the bundle-system is not accompanied by any marked modification of outer conformation; the leaf is even accuminate, while in some species with a median bundle the apex of the leaf is emarginate (*e.g.*, *G. venosum*). This inconstancy of arrangement of the vascular bundles is particularly interesting as occurring in the Gnetaceæ. It is well known that a single median bundle is not as a rule to be found in the leaves of the Gymnosperms.† Here in one genus (Gnetum), which approaches the Dicotyledons so markedly in the character of its leaves, the gap is bridged over by the presence in some species of a single median bundle, as in so many Dicotyledons, while in one species (or more) with a similar external conformation of the leaf, the median bundle is absent, and the vascular system thus conforms rather to the type of most Gymnosperms.

Other cases such as this, which also occur, though in a less clearly defined manner,‡ show how insecure are those attempts, so frequently made, to solve morphological problems by reference to the position of the vascular bundles.

Welwitschia mirabilis.

In the cotyledons, from the period of ripeness of the seed, the growth is intercalary, and not specially localised at any point. It results in the formation of a flattened

* A similar observation has been made by STRASBURGER, 'Conif. u. Gnet.,' p. 115.

† WARMING, 'Recherches et remarques sur les Cycadées,' pp. 22, 23.

‡ Compare the cotyledons of *Cycas* above described, those of *Zamia* (WARMING, *l.c.*, Taf. 3, fig. 28), and of certain Dicotyledons (DE BARY, 'Vergl. Anat.,' p. 246, &c.).

organ, without any midrib, and with a venation similar to that already known for the plumular leaf (compare DE BARY, 'Vergl. Anat.,' fig. 145).

The *plumular leaves* are first formed after germination begins, as a pair decussating with the two cotyledons. The first stages of their development have not been traced, but in seedlings about six weeks old, in which the plumular leaves are still very small, it may be clearly seen that their mode of growth already proceeds according to the same system as is maintained throughout the life of the plant. Longitudinal sections of such a seedling show that the tissues at the apices of the young leaves have already lost their meristematic activity, while spicular cells are already to be seen embedded in the parenchyma (Plate 40, fig. 52). Passing downwards from the obtuse apex of the plumular leaf towards its base, it is seen that the tissues become constantly more active, while at the extreme base divisions by walls perpendicular to the organic axis of the leaf follow in quick succession, and show that the leaf, while still small, owes its increase in length to the activity of a well-marked basal intercalary zone. In such young leaves cut in median longitudinal section (Plate 40, fig. 53) the tissues are seen to be arranged in regular layers, about ten in number, including the epidermis: no periclinal divisions appear in these layers, as a rule, during their development into mature tissue, so that they may be distinctly followed up into the more mature parts of the leaf. As the plant grows older there is an increase in the number of active layers in the intercalary zone, and therefore also in the mature portions of the older leaf. Thus in sections from an old plant it was found that the total number of layers was about 26.

This increase in thickness is quite eclipsed by the increase in width of the whole leaf. As seen in fig. 52, the base of the leaf where it is inserted on the axis is the widest part of the whole leaf; in older plants the width of the mature portion of the leaf exceeds that of its insertion to a slight, but not very marked, degree. Thus there is but slight growth in the direction of the surface of the leaf as the tissues become successively developed. This being the case, sections through the base of the leaf will give a true indication of the distribution of the growth which brings about the increase of width of the leaf as the plant grows older. A series of such sections is represented in Plate 40, fig. 54, *a-d*: (*a*) shows the young plumular leaf about the same age as in figs. 52 and 53, with the two first vascular bundles already developed (i, i); in (*b*) a second pair of bundles is to be seen (ii, ii) between the margin and the first pair; in (*c*) a third pair (iii, iii) has appeared in a similar position; in (*d*) the three pairs are still to be seen, but between them other bundles have now been intercalated.

On comparing these sections closely it will be seen that there has been a constant increase in distance between the bundles of the first pair. The same is the case with other parts of these sections, and a comparison of sections shows a continued but not rapid division of cells perpendicular to the surface. This transverse growth is not

localised at any point in the section, but as a comparison of *a–d* will show, is almost uniform throughout.

For comparison with the leaf of *Welwitschia* some observations were made on the development of the phylloclade of *Ruscus androgynus*, with the result that in the main points there was found to be a close correspondence between them. In *Ruscus* the apical part of the phylloclade soon lost its meristematic activity, and the further growth was localised in the basal part of the organ, both in a longitudinal and transverse direction. Even the vascular bundles showed some similarity of arrangement, two lateral bundles being in advance of the rest. The only essential difference between the two structures is their point of origin relatively to the other members of the plant.

Ephedra distachya.

In order to complete the series, observations were also made on the leaves of *Ephedra distachya*, which are borne in whorls of three; the upper part of each leaf is linear, but the basal part is winged, and the leaves of each whorl are united by the wings into a sheathing base. The development of the leaves is simple. Longitudinal sections of the apical bud show that the leaves arise as separate, lateral, conical protuberances on the conical apex; the growth and cell-division are at first uniform. When the young leaves have advanced so far as to overtop the apex of the stem, active meristematic division at the apex of the leaf ceases, but it is continued at the base. This becomes still more apparent in older leaves. Thus the greater part of the leaf owes its origin to intercalary growth at or near the base of the leaf. This is accompanied by a winged development at the base, the growth extending to that part of the axis which intervenes between the members of one whorl: thus the sheath-like structure above noted is the result. Tranverse sections (Plate 40, fig. 55, i.–iv.) show that the leaf is here also essentially a winged structure, though the wings are reduced: still the similarity between this leaf and that of *Gnetum* and many *Coniferæ* is not difficult to trace.

For the development of the elongated cotyledons no material was at hand, but I should conclude from the structure of almost mature ones, as well as from their mode of growth during germination, while the seed is still retained at their apex, that they increase by intercalary growth.

Conclusion.

It remains to draw together the results which have been obtained from the investigations above detailed. We are now in a position to state the characters of the phyllopodium in the lower forms of vascular plants, and then to follow those characters through the intermediate forms, and trace their modification as we progress towards

those plants which are universally accepted to be higher in the scale. And first it will be well to consider those of the vascular plants which, in the characters of the vegetative organs, as also in other respects, appear to constitute a natural series, viz.: (1) the *Leptosporangiate Ferns*, exclusive of the *Osmundaceæ*; (2) the *Osmundaceæ*; (3) the *Marattiaceæ*; (4) the *Cycadaceæ*. These may, for convenience, be called the large-leaved vascular Cryptogams and Gymnosperms.

In the *Hymenophyllaceæ*, in which group of Ferns the conformation of the leaf is simplest,* the phyllopodium is not clearly differentiated from the appendicular members of higher order. It arises at first as a flattened organ, referable in its external conformation (according to PRANTL's figure), as well as in the arrangement of the cells at its apex, to a single plane; by increase in bulk of its central part, below the extreme apex, and by continued growth at the margins, it becomes a typical winged structure. PRANTL (*l.c.*, p. 59) regards it as probable that in the simplest forms there was "an entirely unbranched leaf, traversed only by a midrib, a form which probably really exists in the simplest species of *Hymenophyllum*." I think, however, judging from the rather incomplete data given by PRANTL, that it is more probable that the leaf was originally a flattened expansion without a midrib, and that the appearance of the median thickening was of subsequent occurrence. This is, however, pure theory, and, in the absence of intermediate forms between the Ferns and the Muscineæ, it is incapable of decision.

The branching of the phyllopodium in the *Hymenophyllaceæ* is chiefly, if not exclusively, *dichotomous*. On advancing from the simpler to the more complex forms, a transition may be traced from the typically dichotomous to the sympodial development (PRANTL, *l.c.*, p. 58), and this is accompanied by an increasing prominence of the phyllopodium, which is thus a pseudo-axis. Though prominent to the eye, the phyllopodium is not in these cases clearly differentiated in the first instance from the less strongly developed branches of the dichotomy: it is often winged like them to its extreme base, while it shows no sheathing development, nor other peculiarity of conformation at its base.

Passing on to the *other Leptosporangiate Ferns* (exclusive of the *Osmundaceæ*), though the apex of the phyllopodium is often more bulky than in the *Hymenophyllaceæ*, it still retains the two-sided apical cell, so characteristic of flattened organs, and thus in the arrangement of its meristem is referable to one plane. When mature, it is typically a winged structure throughout its length, and though in Ferns with much branched leaves the wings are often but slightly developed in the lower parts of the phyllopodium, in Ferns which have more simple leaves the winged development may be readily followed to the point of insertion on the axis. As regards the

* The question may for the present be left open as to the real relation of the Hymenophyllaceæ to other Leptosporangiate Ferns, *i.e.*, whether they are rudimentary forms or reduced representatives of a higher development. It is sufficient for the present that the leaf as there represented is structurally the simplest among the large-leaved forms.

branching of the phyllopodium, it is in many cases undoubtedly *monopodial*, though in the higher ramifications there is frequently a return to the dichotomous mode of branching. As is well known, the apical growth in some cases may be unlimited (*Lygodium*). Thus in the majority of the Leptosporangiate Ferns the phyllopodium is more clearly differentiated from the members which it bears than is the case in the *Hymenophyllaceæ*, and this is most clearly marked by the prevalence of a monopodial branching at least in the earlier ramifications. But the structure of the apex is still that characteristic of flattened organs, and when dichotomy occurs in its higher ramifications, it is no more distinct from the members of higher order which it bears than is the case in the *Hymenophyllaceæ*.

In the phyllopodium of the *Osmundaceæ* the two-sided apical cell as found in other Leptosporangiate Ferns is replaced by a *three-sided, conical, apical cell*, and it is believed that these are the only plants in which a three-sided cell has been found at the apex of the leaf.* Thus the arrangement of the apical meristem is that characteristic not of flattened, but of cylindrical organs, and this may be regarded as indicating an advance in robustness of character, and therefore in adaptation to serve as a supporting organ. But the change is not accompanied by any marked difference of external conformation of the phyllopodium as a whole: it is still a winged structure, though the wings cannot be traced in the lower parts of the leaf as originating from any definite marginal series of cells. The position of the apical cell is such as to correspond to the requirement of a more bulky development of the phyllopodium on the dorsal side, the greater part of the tissues derived from the two dorsal series of segments being devoted to the building up of the bulky dorsal part of the phyllopodium, while the wings and pinnæ are derived partly from the edges of the dorsal segments, partly from the ventral segments. It is clear that a three-sided apical cell is better adapted to a leaf with a bulky winged phyllopodium than a two-sided one, and in this sense the structure of the apex of the phyllopodium in the *Osmundaceæ* may be regarded as an advance upon that in other Leptosporangiate Ferns. The branching of the phyllopodium in the *Osmundaceæ* is *monopodial*, and no example of dichotomy has been observed in the higher ramifications, at least in *Osmunda regalis*: thus the phyllopodium preserves its identity throughout the leaf, as distinct from the pinnæ which it bears; and this is not the case in those Leptosporangiate Ferns in which it branches dichotomously. At the base of the phyllopodium there are peculiar modifications of the winged structure, which will be discussed again later.

In *Angiopteris*, as an example of the *Marattiaceæ*, there is no single apical cell occupying the bulky apex of the phyllopodium, but a group (four) of apical cells give rise, by their repeated divisions, to the tissues of the leaf, which thus approaches in the arrangement of its apical meristem to that characteristic of the higher plants. The apex of the phyllopodium is not flattened, but cylindrical-conical, and its internal

* HOLLE asserts that there is a wedge-shaped cell at the apex of the leaf of *Angiopteris*, and describes it as being of "irregular cross-section": on this point compare my own observations as above detailed.

structure is in accordance with this. At the base of the leaf peculiar modifications are more prominent than in the *Osmundaceæ*, while in the upper part of the phyllopodium traces of a winged development can only be made out with difficulty. Its branching is exclusively monopodial, and its growth in length is, in some cases at least, strictly limited, the phyllopodium terminating in a blunt, rounded cone.

Finally, in the *Cycadaceæ* the apex of the phyllopodium is covered by a clearly marked layer of dermatogen; its growth is never very conspicuously apical, though in *Cycas*, and perhaps in *Dioon*, it is more so than in other genera; after the first stages are past, the growth is exclusively intercalary. It is from the first a bulky, rounded structure, but it bears in most cases well-marked and comparatively bulky lateral wings, extending from base to apex, and widened in the lower portions to form a sheath. The branching is in all cases *monopodial*, but the order of development of the branches is often basipetal.

Drawing together these facts, it is clear that in the above series of plants there may be traced a progressive differentiation of the phyllopodium as a supporting organ on the one hand, and of the other members of higher order which develop as flattened expansions on the other. In the *Hymenophyllaceæ* the difference appears to lie merely in the stronger development of a certain branch of each dichotomous system, while other branches, similar to them in origin and conformation, are of more limited growth, and assume a lateral position: gradually a monopodial mode of branching becomes prevalent (most Leptosporangiate Ferns); this shows a difference from the very first between the podium and the members of higher order which it bears, but the difference is again lost where there is a return to the dichotomous mode of branching. The next step is that the apex of the phyllopodium loses the structure characteristic of flattened organs, and assumes that characteristic of cylindrical structures (*Osmundaceæ*), and this is maintained during the development of the lower portions, though in its upper parts the phyllopodium is reduced to a flattened structure not unlike, in form and structure, that in other Leptosporangiate Ferns. In the *Marattiaceæ* the apical growth is arrested, at all events in certain cases, at a comparatively early stage: the phyllopodium has the apical characteristics of a cylindrical organ, and where its growth is limited it does not resume the characters of a flattened organ; it is essentially an organ adapted rather to bear the flattened assimilating organs, than such an organ itself, while by its exclusively monopodial branching it is always clearly distinguished from the branches (pinnæ) which it bears. Finally, in the *Cycadaceæ* the distinctive characters of the phyllopodium are still more accentuated; it is from the first a bulky structure; its apical growth is soon arrested; it does not (except in a few cases, *e.g.*, some leaves of *Stangeria*) develop as a flattened assimilating organ, but differs both genetically and in its further development from the pinnæ which it bears. It is essentially an organ adapted to bear the members of higher order, on which the assimilating function mainly devolves.

It is unfortunate for the study of the comparative morphology of the shoot that no

plants intermediate between the *Muscineæ* and the *Filicineæ* have been found living upon the earth, which might give a key to the origin of the morphological differentiation of the sporophore. The series passes at a single plunge from cellular structures, with no differentiation of axis and leaf (sporogonia), to vascular plants, with a well differentiated axis and leaf: thus we can only speculate by analogy as to the mode of origin of the differentiated stem and leaf in vascular plants. The analogy of the morphological differentiation of the oophore in the leafy *Muscineæ* is well known, and too often applied as though the "leaf" in that group were the homologue of that in the vascular plants. I think that, in the above comparative study of the differentiation of the phyllopodium from the pinnæ which it bears, we have presented to us a truer analogy than that of the *Muscineæ*. May we not with good reason think that, just as the phyllopodium gradually asserts itself as a supporting organ among structures originally of similar origin and structure to itself, so also the stem may have gradually acquired its characters by differentiation of itself as a supporting organ from other members originally similar to itself in origin and development? Thus the stem and leaf would have originated simultaneously by differentiation of a uniform branch-system into members of two categories, and this is what is actually illustrated, in the case of the phyllopodium and pinnæ, in the series of plants above discussed.

The most prominent change to be seen in the mode of development of the leaf on passing from the Ferns to the higher vascular plants is the restriction of that apical growth which is so prominent a characteristic of Ferns, and consequently the greater prominence of the intercalary growth in those of the higher plants which have comparatively large leaves. The observations detailed above show that while the phyllopodium of the Leptosporangiate Ferns has a continued apical growth, which is sometimes unlimited, that of *Angiopteris* is, at least in some cases, arrested at a comparatively early period: again in *Cycas*, and probably in *Dioon*, the growth at the apex and acropetal development of the pinnæ are continued for a short time, while in most other *Cycadaceæ* the apical growth ceases at a still earlier period.

Thus there are intermediate steps between the Ferns with continued apical growth of the leaf, and the higher plants in most of which that apical growth is arrested at an early period.

In the Ferns the intercalary growth is carried on simultaneously with apical and marginal growth, and thus does not play such a prominent part in moulding the form of the mature leaf of those plants. But in the higher vascular plants the growth at the extreme apex and at the margin is usually arrested at a comparatively early stage, and the effect of the intercalary growth more or less strictly localised, which brings about various displacements of the original position of members, often becomes more apparent, or is even actually greater than in the Ferns. It is chiefly by the variations of external form of the leaf, resulting from various distribution of intercalary growth, that the leaf of the higher plants acquires its prominent characteristics; and it is mainly owing

to this that the branched leaf has so long been treated as one member, and not as a branch-system. Differences of localisation of intercalary growth are regarded as of but secondary importance in the morphology of axes, and they should be regarded in the same light in the morphology of leaves: the neglect of this principle has resulted in the division of the primordial leaf into the *foliar base* (blattgrund) and *upper leaf* (oberblatt), two categories which, as I have pointed out in the introduction to this essay, are not morphologically co-ordinate in the case of branched leaves.

With the more complete differentiation of the phyllopodium and the pinnæ there appears also a differentiation of the parts of the phyllopodium itself, corresponding to and foreshadowing that more complete differentiation which is found among the higher vascular plants. There, as above pointed out, three parts of the phyllopodium may be distinguished: the *hypopodium* which coincides with EICHLER's "blattgrund;" the *mesopodium* or petiole; and the *epipodium*, which includes the upper part of the phyllopodium with its wings, but exclusive of its branches of higher order. That these are parts only of one podium, and not fundamentally different parts, as EICHLER would have it (*l.c.*, p. 25), appears to me to be strongly supported by a comparative study of the leaves in the series of plants above treated in detail. As I have repeatedly pointed out, the phyllopodium is fundamentally a winged structure throughout its length, though the wings are not uniformly developed, and are sometimes partially or entirely (*Pilularia*) suppressed. In the plants of this series which have the simplest structure (*Hymenophyllaceæ*) the different parts of the phyllopodium are not distinguishable; its development is almost uniform throughout. In the majority of the Leptosporangiate Ferns their differentiation is but slight, though in some forms—for instance, *Aspidium Filix-Mas* and *Onoclea germanica*—a somewhat distended basal portion may be distinguished from the upper parts of the phyllopodium. In *Osmunda* the distinction of the basal part or hypopodium is more marked, the lateral wings being more bulky and extended; in *Todea* the winged development is not exclusively lateral, but is continued transversely across the face of the phyllopodium, so as to form a conspicuous sheath; but this continuation is only formed at a comparatively late stage. In *Angiopteris* it is present from a very early period, and is closely connected with the formation of the "stipules." By means of *Todea* an explanation is afforded of the probable nature of the stipule in *Angiopteris*. As I have above pointed out, it may with good reason be regarded as an advanced modification of that winged conformation, so clearly seen at the base of the leaf in other Ferns. A similar explanation will serve also for *Ceratozamia* and *Stangeria*.* In other forms, especially among the *Cycadaceæ*, the base of the phyllopodium shows

* The extension of the stipular development transversely across the face of the phyllopodium is not an isolated morphological fact: a similar extension is also to be found in the development of orbicular leaves, such as *Hydrocotyle*, *Tropæolum*, &c. This has been clearly shown by GOEBEL ('Vergl. Entw.,' p. 234). It will remain for future observations to show how far a similar comparative treatment may be applied to the stipules of Dicotyledons.

characters resulting from distention, &c., but the variation from the winged structure is less marked; still in many cases the distinction is apparently accentuated by the abortion of the upper parts of the leaf, as in the *scale-leaves,* in which a correspondingly greater lateral extension is found. But this apparent accentuation of the difference between the hypopodium and the upper part should not cloud our morphological vision; the real nature and origin of the hypopodium remain the same, whatever variety there may be in the details of its development in the individual leaf. The distinction between the mesopodium and epipodium is never very clearly marked in the plants under consideration. Thus, though in these lower forms the differentiation of the parts of the phyllopodium is not so complete as in many Angiosperms, there may still be traced an increasing clearness of their differentiation on passing from the simplest forms upwards.

A similar comparative study of the series of large-leaved Vascular Cryptogams and Gymnosperms shows that progressive changes may be noted in the order and mode of origin of the pinnæ on the phyllopodium. In the lower forms of the series the order of their appearance is strictly *acropetal,* whether their origin be by dichotomy, as in the *Hymenophyllaceæ,* &c., or by monopodial branching, as in *Osmunda, Angiopteris,* &c. This acropetal order of appearance may be traced as feebly represented in *Cycas* and *Dioon* among the *Cycadaceæ;* but even in these forms there is also a simultaneous *basipetal* order of development of the lower pinnæ which is more prevalent in most of the genera of the *Encephalarteæ,* to the exclusion of the acropetal order of succession: thus in *Macrozamia, Ceratozamia, Zamia,* and *Encephalartos* the order of succession of appearance of the pinnæ is exclusively basipetal, and since the phyllopodium ceases its apical growth after the appearance of the first pinnæ, subsequent elongation is due to intercalary growth. Such a mode of development is not without its parallel among the *Angiosperms.* GOEBEL cites, as examples of a basipetal order of development of pinnæ, the leaves of *Myriophyllum, Ceratophyllum, Rosa canina, Potentilla reptans* and *Anserina, Spiræa lobata,* &c.; and he further points out that the order of succession is not even constant in one and the same genus, as is seen on comparing *Spiræa Lindleyana* with *Spiræa lobata* ('Vergl. Entw.,' p. 227). These irregularities in order of succession, accompanied by intercalary growth of the phyllopodium in length, may further be compared with those examples of similar development cited as occurring among the *Phæophyceæ* (GOEBEL, *l.c.,* p. 186). It may be noted that the arrest of the apical growth of the phyllopodium, and the tendency to develop the pinnæ in a basipetal succession, progress simultaneously in our series of large-leaved Vascular Cryptogams and Gymnosperms, and it can hardly be doubted that the two phenomena are mutually connected.

In most of the Leptosporangiate Ferns the pinnæ arise as more or less flattened structures, derived from the marginal series of cells, while some of the neighbouring cells also take part in the process: in other words they arise along the lines where the wings of the phyllopodium are, or will ultimately be. Though, as was shown by KNY,

each pinna does not correspond to one segment of the two-sided apical cell, still the pinnæ have a definite relation to the apical cell and its segments, each longitudinal row of pinnæ originating from one of the two series of segments cut off from the two-sided apical cell. In the *Osmundaceæ*, since there are but two series of pinnæ as before, but *three* series of segments of the apical cell, the relations of the former to the latter cannot be the same. In this group the two series of pinnæ correspond in position to two of the angles of the three-sided cell, and the individual pinnæ are derived partly from tissues originating from the ventral series of segments, partly from the dorsal.

Again, comparing the members of our series, there is to be traced a progressive increase in bulk of the individual pinna. In *Ceratopteris* the young pinna is a thin flattened structure: in many Ferns, as *Aspidium Filix-Mas*, *Polypodium vulgare*, &c., the first formed pinnæ are more bulky, but still a marginal series of cells may easily be seen upon them: in *Osmunda* not only are the young pinnæ more rounded, but also no marginal series of cells are to be found on those first formed, while they remain young. In *Angiopteris* and the *Cycadaceæ* the pinnæ appear as hemispherical papillæ of tissue, on which no marginal series of cells are to be found. In all these plants the pinnæ are formed on the more or less developed wings of the phyllopodium. There is thus a progressive increase in bulk of the pinna in its first stages, which may be traced on passing upwards through our series.

Parallel with the increase in bulk of the pinnæ there is also an increase in bulk of the wings of the phyllopodium, pinnæ, and pinnules, &c., in those cases where a winged development takes place. Thus in the *Hymenophyllaceæ* the wings consist for the most part of but a single layer of cells, though in some species they consist of more than one (PRANTL, Hymenophyllaceen, p. 23), still the structure is in all cases very simple. In the majority of Ferns a marginal series of cells can be clearly recognised on the young pinnæ or pinnules, &c., which give rise by their growth and divisions to a wing-structure consisting of but few layers of cells: in *Angiopteris* no such marginal series is apparent, and the whole structure of the wing is more bulky and complicated than in the Leptosporangiate Ferns: repeated periclinal divisions are found in the superficial cells of the wing during development. In *Cycas* the wings arise to external appearance in a manner not unlike those of *Angiopteris*, but there is between the two this important difference: that the periclinal divisions in the superficial cells are entirely absent in *Cycas*. Thus again in the complexity of the structure of the wing a progressive advance is seen on passing upwards through our series of large-leaved plants, an advance from a simple structure to that more complicated structure which is characteristic of the higher plants.*

In the above paragraphs a number of characters have been brought forward, showing an almost uniform progress of complexity and differentiation of the vegetative organs,

* The case of the genus *Todea* should be mentioned as exceptional, while *Todea barbara* has wings consisting of about nine layers of cells, *Todea superba* has wings with only one or two layers, it thus

from the Leptosporangiate Ferns, through the *Osmundaceæ* and *Marattiaceæ* to the *Cycadaceæ,* and there is no apparent objection on other grounds to thinking that these plants constitute a natural series; in other words, that they indicate, at least roughly, a line of natural descent. If this be so we are confronted by a remarkable fact. It has been repeatedly insisted upon that the characters of the vegetative organs of *Angiopteris* approach very closely to those of certain *Cycadaceæ.* Yet between the two there is all the difference in the reproductive organs between the characteristic free prothallus and antherozoid of the Vascular Cryptogams, and the endosperm and pollen-tube of the Gymnosperms. This is one of the most striking examples in the vegetable kingdom of the non-parallelism in progress of the vegetative and of the reproductive organs : here while there is comparatively little progress in the vegetative organs from the *Marattiaceæ* to the *Cycadaceæ,* the sexual reproduction shows that great advance from the process characteristic of the vascular Cryptogams to that typical of the higher plants. The converse of this non-parallelism is also to be found at a different point in the vegetable kingdom, viz. : a persistence of the reproductive characters, while a great advance is made in the differentiation of the vegetative organs; for example, between the *Muscineæ* and the *Filicineæ* there is all the difference in the differentiation of the vegetative organs of the sporophore, between a cellular structure without axis and leaf, and the simplest form of Fern plant; but meanwhile the sexual processes remained unaltered, there being no fundamental difference between the archegonium and the antherozoid in the *Muscineæ* and the similar organs in the *Filicineæ.* Other examples might be brought forward of this non-parallelism, but the two converse cases named are the most prominent in the vegetable kingdom.

This paper has hitherto dealt for the most part with comparatively large and complicated leaves; a word must now be said on the leaves of simpler organisation found among the Vascular Cryptogams and on the application of the method of treatment which I have proposed to them also. Some of the simpler forms of leaf may show little preponderance of growth in any given direction; this is the case in *Azolla* and *Selaginella.* To such leaves the application of the term phyllopodium is obviously unnecessary and unsuitable. In other cases the leaf may be of very simple organisation, but still show a distinct preponderance of growth in a given direction, as in *Pilularia, Lycopodium,* many *Coniferæ* and *Gnetaceæ,* and to a slight degree *Salvinia.* Here we may recognise a simple unbranched phyllopodium, which may be winged (*e.g., Gnetum,* &c.), or cylindrical (*Pilularia*), or flattened (*Welwitschia*). If such a leaf were to show the characteristic differentiation of those parts, we might distinguish them as the hypo-, meso-, and epi-podium; thus, for instance, in *Isoetes,* in which, as pointed out by GOEBEL (Bot. Zeit., 1880, p. 785), the basal part (hypo-

approaches the *Hymenophyllaceæ* in this character, though its sporangium is similar to that of other *Osmundaceæ.*

podium) is to be distinguished from the upper part of the leaf (epipodium);* and again in *Gnetum Gnemon,* where the winged epipodium may be distinguished from the mesopodium or petiole, and this is slightly different in conformation from the swollen basal portion or hypopodium. Such distinctions are only to be drawn where they are warranted by the exigencies of description: EICHLER asserted that the distinction of "blattgrund" and "oberblatt" is common to the leaves of all Phanerogams; † such a general application is as unnatural and prejudicial as was the general application of the spiral theory of leaf-arrangement.

Finally, there remain those more complicated forms of leaf which are not included in the series of large-leaved Vascular Cryptogams and Gymnosperms above described. The well-known development of the leaf in *Marsilia* corresponds in many respects to that of the typical leaf in the Ferns; it may be regarded as a reduced type connecting them with the still further reduced members of the *Hydropterideæ.* The leaf consists of a phyllopodium bearing four pinnæ, of which the lower pair are formed by monopodial branching, while the upper pair are described as being the result of bifurcation of the apex of the leaf. In *Botrychium Lunaria,* in which the details of arrangement of the meristem, and other points in the development of the foliage-leaf are but imperfectly known, there is a well-marked phyllopodium, preserving imperfectly the characters of a winged structure. It bears pinnæ in two longitudinal rows; the order of their development is stated by HOLLE (Bot. Zeit., 1875, p. 274) to be acropetal, and this coincides with my own limited observations. In the mode of development, external conformation, and arrangement of the pinnæ it is not unlike *Zamia.* The apex of the leaf frequently terminates in an equal pair of pinnæ, which recalls the similar arrangement in *Marsilia,* and further the leaf of *Ginkgo;* but frequently there is a somewhat flattened terminal process, which projects beyond the last pinnæ; such forms constitute an instructive series connecting a decidedly monopodial branching with cases of apparent dichotomy. In *Ophioglossum* the phyllopodium is not branched, its apical part developing as a flattened expansion. In *Helminthostachys* it is branched, but details of the development of the leaf have not yet been published.

The foregoing pages will have amply shown that the more complicated forms of leaf among the Vascular Cryptogams naturally lend themselves, *throughout their whole length,* to a consistent morphological treatment as branch-systems; while in those

* The leaf of *Isoetes* shows intermediate characters between those of *Angiopteris* and of the *Cycadaceæ.* There is no apical cell, and apical growth is not strongly defined; periclinal divisions of superficial cells are frequent throughout the leaf, from apex to base, but especially on the ventral side; intercalary growth is strongest at first below the ligule, and then diminishes in that part, and extends to the upper part of the leaf. These characters as well as others suggest that *Isoetes* may be a form intermediate between the *Marattiaceæ* and *Cycadaceæ,* in which the vegetative organs have been reduced in structure and external form in accordance with its aqueous habit.

† *l.c.,* p. 7: "Zwei Haupt-theile, die allen phanerogamischen Blättern gemeinsam sind."

simple cases where there is growth in a given direction, but no branching occurs, the characters of the simple leaf are not unlike those of the phyllopodium as described for the more complicated forms. Further, it has been shown that as we rise in the scale of the *Gymnosperms*, gradual modifications of the characters become apparent; for instance: (1) there is a gradual differentiation of the main axis of the leaf (the phyllopodium), as a supporting organ, from the members of higher order (pinnæ) which it bears; (2) peculiar conformations appear at the base of the phyllopodium, such as sheaths, and stipules; (3) there is an earlier arrest of the continued apical growth, and increased prominence of intercalary growth; (4) there is an increased robustness of the several parts, which may be recognised clearly on their first appearance. All these characters lead on gradually towards the leaf as it is seen in the *Angiosperms*, and more especially in the *Dicotyledons*. On these grounds I conclude that the leaf in the latter plants should also be treated consistently as a simple branch or branch-system, *throughout its whole length*, however greatly the prevalence of intercalary growths in various directions, and at various points, may displace and distort the original arrangement of the parts. It has also been shown that the modifications at the base of the leaf do not exist, or are hardly to be traced in the Leptosporangiate Ferns, and that where they are found in higher forms they may be referred to modifications of contour of the fundamental winged structure; on this ground it is concluded that such modifications, however prominent they appear in the higher plants, are not of such a fundamental nature as to justify the division of the leaf in the first instance into two parts (foliar base and upper leaf), which are, as I have above pointed out, *not morphologically co-ordinate* where a branching of the leaf occurs.

It will be noted that the treatment of the leaf as a simple podium or as a branch-system implies a distinction between the *wings* of a phyllopodium and the *pinnæ*, and it may be argued that such a distinction cannot be clearly defined: for instance, the wavy margin of the leaf of *Ginkgo* and of the pinnæ in species of *Zamia*: are the projections in these cases to be regarded as members of higher order? I can only reply to this that difficulties of this nature beset every morphological generalisation, and that in my opinion the number of cases in which such difficulties come prominently forward is not sufficient to justify the rejection of the system which I have proposed.

I cannot close this paper without acknowledging how much I am indebted to the Director and Assistant Director of the Royal Gardens at Kew, not only for the use of the JODRELL Laboratory, but also for the unstinted supply of the rare material which alone could make this investigation possible.

Description of Figures.

PLATE 37.

Pilularia.

Fig. 1. Apex of the stem of *Pilularia globulifera.* *ap.* Apex. 1, 2, 3–7. The successive leaves. b_1–b_7. The successive buds. r_3–r_6. The corresponding roots. ×70.

Fig. 2. Dorsal side of a similar apex with two young leaves (1–2), and bud b_2 seen obliquely. ×175.

Fig. 3. Leaf (l) and corresponding bud (b) of *Pilularia.* *h, h.* Hairs. ×325.

Osmunda.

Fig. 4. Arrangement of cells at the apex of the leaf of *Osmunda regalis:* the arrows show the median plane of the leaf, and point towards the apex of the stem. ×175.

Fig. 5. Apex of the leaf of *O. regalis,* with the two last-formed pinnæ (p_5–p_6); the leaf has already assumed the circinate vernation, which accounts for the apparently unsymmetrical position of the apical cell. ×130.

Fig. 6. *Osmunda cinnamomea.* Apex of the leaf before the first pinnæ appear, showing the relation of the wings (w, w) to the segments of the apical cell. ×70.

Todea.

Fig. 7. Apex of the leaf of *Todea superba,* showing the segments of the apical cell with their sub-divisions less regular than in *Osmunda.* ×175.

Fig. 8. Sections of the leaf of *Todea superba.* *b.* Transverse. *a, c.* Longitudinal and median: these illustrate the origin of the wings (w) at the base. ×20.

Angiopteris evecta.

Fig. 9. Apex of the stem of *A. evecta,* showing a conical apical cell, with its segments. ×175.

Fig. 10. Young leaf of *A. evecta* seen from above; *ap.* is the apex: the arrow points towards the apex of the stem. ×20.

Fig. 11. Rather older leaf seen from the ventral side. ×20.

Fig. 12. Median longitudinal section of the apex of the same leaf of *A. evecta* as is represented in fig. 15. The cells (x, x) are two of the group of four apical cells. ×175.

PLATE 38.

Fig. 13. Cells at the apex of the leaf of *A. evecta*, the apical cells marked (x, x). $\times 175$. The arrows show approximately the median plane of the leaf.

Fig. 14. Another example of the above : the arrangement of the cells is less regular.

Fig. 15. Apex of the leaf of *A. evecta*, which has begun to form three pinnæ. $\times 10$.

Fig. 16. Apical part of a leaf of *A. evecta*, which has formed 9 pinnæ. The lower of these (2 and 3) have already begun to form pinnules. $\times 5$.

Fig. 17. Leaf of *A. evecta* with six pinnæ. The phyllopodium ends abruptly (*ap.*). $\times 4$.

Fig. 18. Transverse section of a pinna of *A. evecta* showing wings (w, w). $\times 20$.

Fig. 19. One of these wings under higher power. $\times 175$.

Cycas Seemanni.

Fig. 20. Endosperm with embryo natural size.

Fig. 21. Transverse section of cotyledons near the base, showing in one case a median bundle, in the other no single median bundle. $\times 10$.

Fig. 22. Longitudinal median section of the apex of a young seedling. $\times 20$.

Fig. 23. Similar section of an older plant. $\times 20$.

Fig. 24. Young leaf, ventral aspect, showing wings continuous from base to apex. $\times 20$.

Fig. 25. Horizontal section of the apex of a plant 12 months old. $\times 20$.

Fig. 26. Leaf of a young plant, showing the wings (w) continuous upwards : note especially that the pinnæ are not in regular succession in respect of size. $\times 20$.

Fig. 27. Leaf showing the pinnæ at the middle of the two series most advanced. $\times 20$.

PLATE 39.

Fig. 28. Similar leaf showing a decided decrease in size of the pinnæ in a basipetal direction : there was in this case no decided proof of the absence of an acropetal order of development. $\times 20$.

Fig. 29. Transverse sections (a) of a scale-leaf, (b) of a foliage-leaf. *Scl.*=sclerenchyma. $\times 10$.

Cycas Jenkinsiana.

Fig. 30. Leaf in which the formation of pinnæ has begun, and showing those about the middle of the two series as most advanced. $\times 20$.

Fig. 31. a and b, the lower ends of the series of pinnæ on two leaves of different ages. $\times 20$. In both cases it is seen that an increase in their distance apart, which is due to greater elongation of the phyllopodium, is coincident with an arrest of development of the individual pinnæ.

Dioon edule.

Fig. 32. Leaf showing pinnæ decreasing successively in size towards both the apex and the base. ×20.

Macrozamia Miqueli.

Figs. 33–5. Successive stages of development of the leaf, showing the origin of the pinnæ in basipetal order. ×20.

Fig. 36. Longitudinal section of a leaf including one lateral row of pinnæ, seen from the inner side. ×20.

Fig. 37. Apex of the phyllopodium of a rather older leaf, with three pinnæ. ×20.

Encephalartos Barteri.

Figs. 38, 39. Successive stages of development of the leaf showing exclusively basipetal order of succession of the pinnæ. ×20.

PLATE 40.

Ceratozamia Mexicana.

Fig. 40. Young leaf with the basal flaps (stipules) removed: transverse connexion of them across the face of the phyllopodium not yet apparent. Basipetal order of succession of the pinnæ. ×20.

Stangeria paradoxa.

Figs. 41, 42. Young leaves before the appearance of the pinnæ. ×20.

Fig. 43. Young leaf, ventral aspect: the sheath has been removed. ×20.

Fig. 44. Apical bud of a young plant, showing the sheathing stipule. ×2.

Fig. 45. Young pinnæ. ×20.

Fig. 46. Ventral aspect of a young leaf, showing two equal pinnæ at apex. ×4.

Gnetum Gnemon.

Fig. 47. Axillary buds; the larger one shows a leaf (*l*) in ventral aspect, with acuminate apex. ×20.

Fig. 48. A bud in longitudinal section, which cuts the two leaves through their median planes. ×20.

Fig. 49. Leaf in dorsal aspect, 1, 2, 3, 4, the points at which the corresponding sections of fig. 50 were cut. ×20.

Fig. 50. 1, 2, 3, 4, successive transverse sections of the leaf at points 1, 2, 3, 4, in the preceding figure, showing the relative position and size of the wings and the midrib. ×20.

Fig. 51. Transverse section through a young wing of the leaf. ×175.

Welwitschia mirabilis.

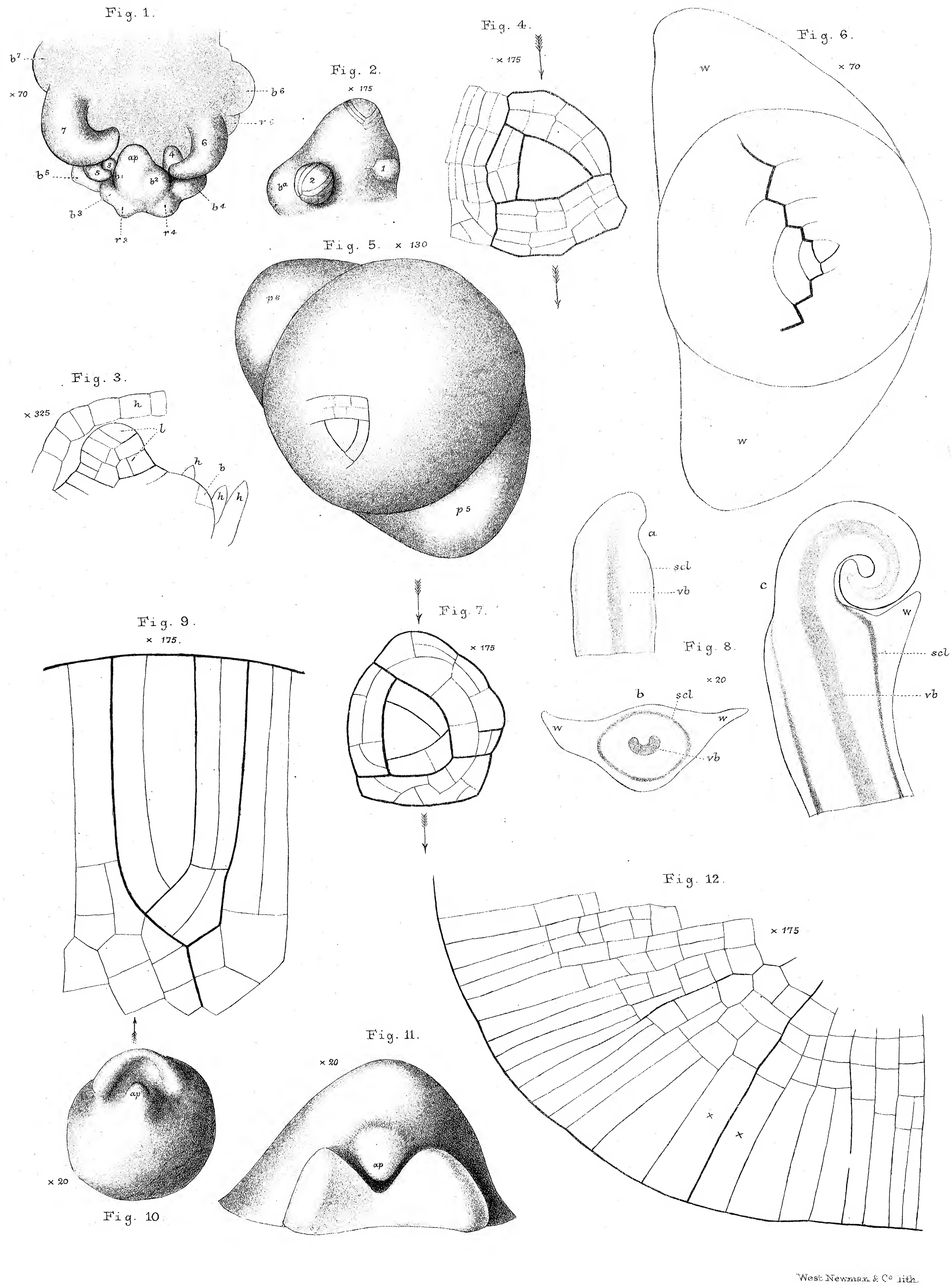
Fig. 52. Longitudinal section of the apex of a seedling about six weeks old, showing one plumular leaf in surface view: the depth of the shading in this and the next figure is intended to represent the relative intensity of growth, and cell-division. ×20.

Fig. 53. Longitudinal section of a seedling about 6 weeks old, in a direction perpendicular to the planes of the plumular leaves. ×20.

Fig. 54. Transverse sections of successively older plumular leaves. ×20. i, ii, iii, indicate the bundles of successively formed pairs.

Ephedra distachya.

Fig. 55. i–iv. Successive transverse sections, from apex to base, of a mature leaf. ×20.



West Newman & Co lith.

Fig. 13. × 175.

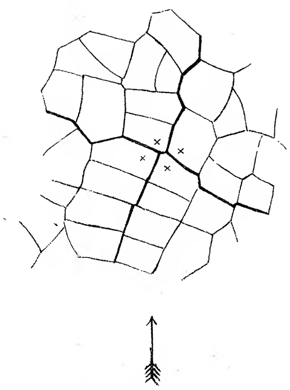


Fig. 14

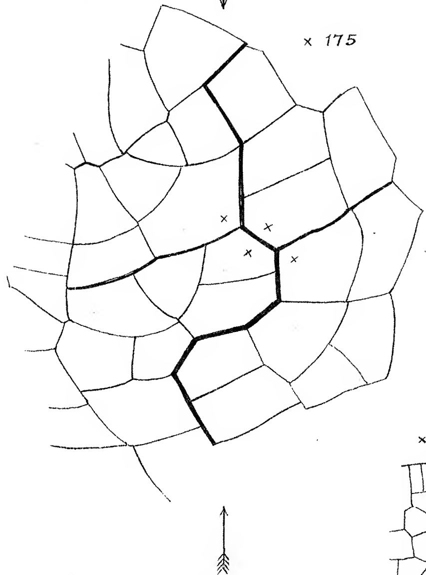
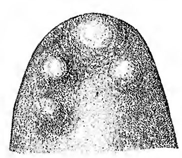
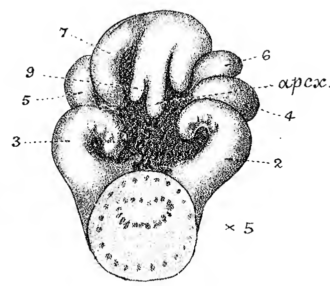


Fig. 15.



× 10

Fig. 16.



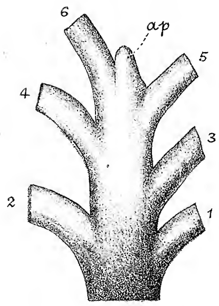


Fig. 17.

× 4.

Fig. 18. × 20.

Fig. 19.

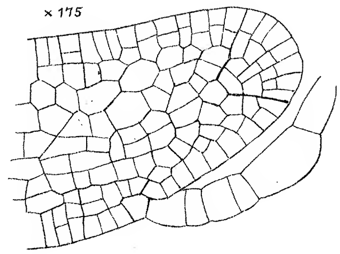


Fig. 20.

nat. size.

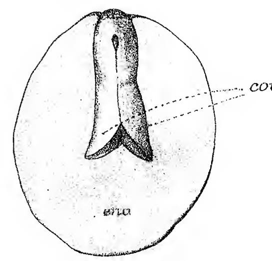


Fig. 21.

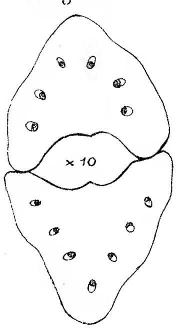


Fig. 22.

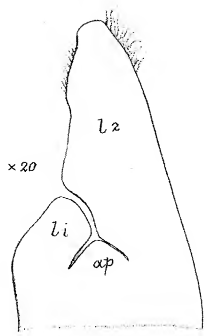


Fig. 23.

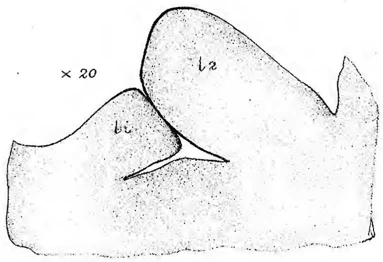


Fig. 24.

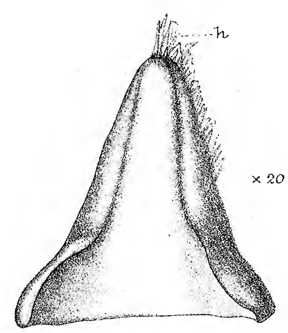


Fig. 26.

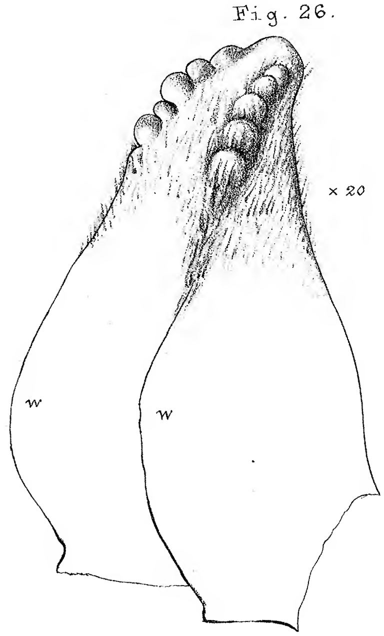


Fig. 25. × 20.

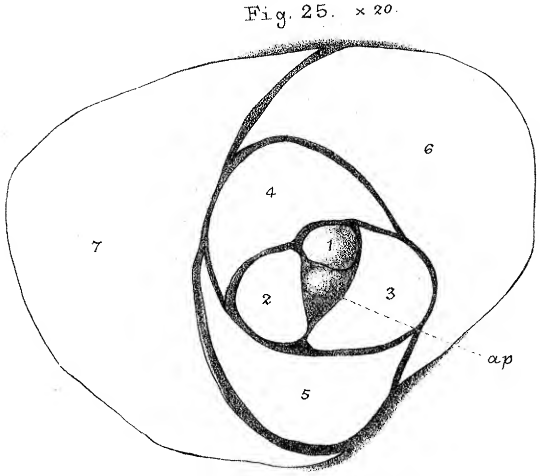
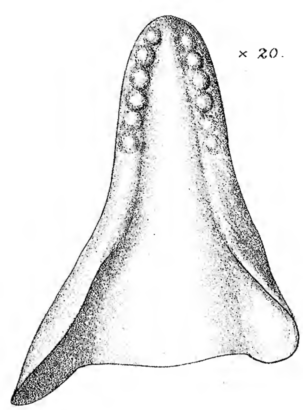


Fig. 27.



West, Newman & Co. lith.

Fig. 29.

× 5

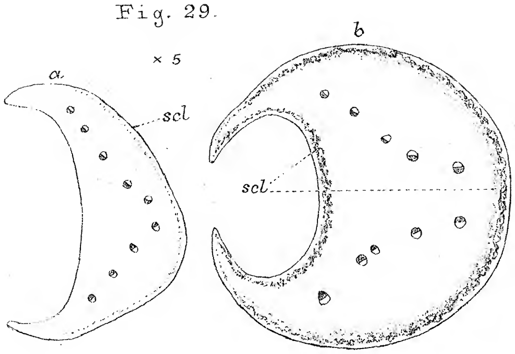


Fig. 28.

× 20.

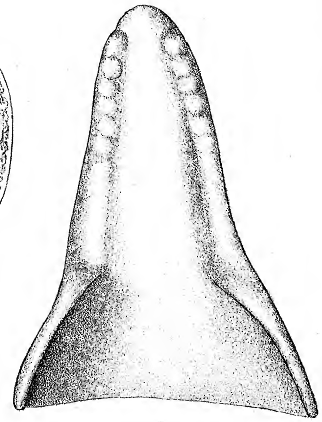


Fig. 31.

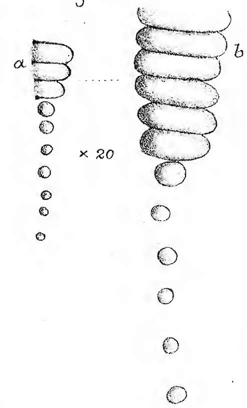


Fig. 30.

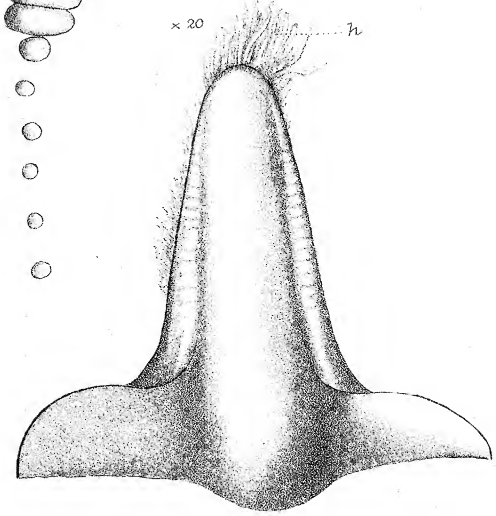


Fig. 32.

× 20

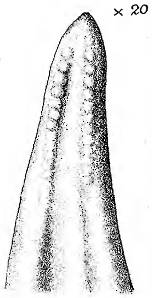
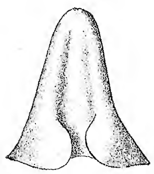


Fig. 33.



× 20

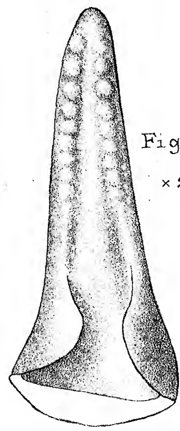


Fig. 34.

× 20

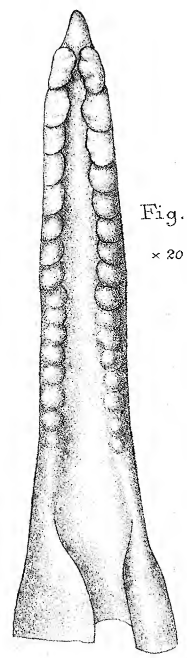


Fig. 35.

× 20

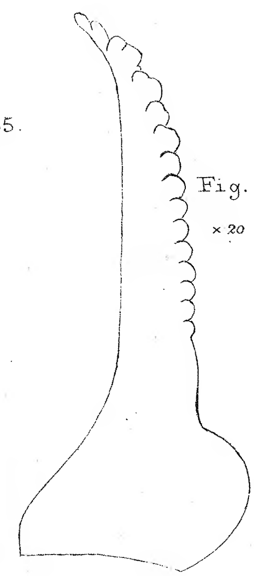


Fig. 36.

× 20

Fig. 38.

× 20

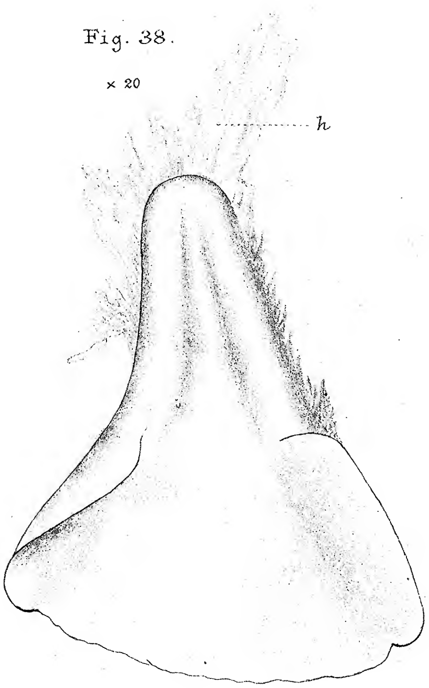
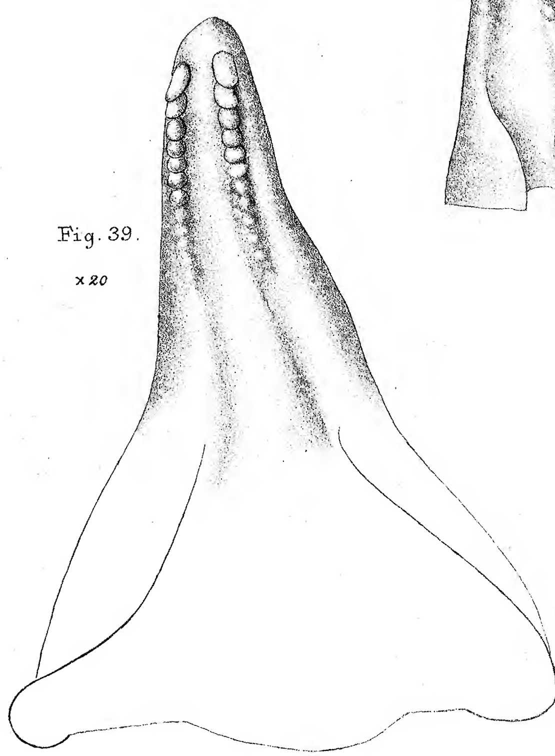


Fig. 39.

× 20



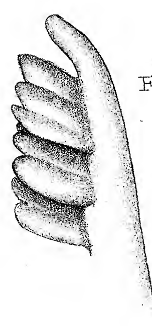


Fig. 37.

× 20

Fig. 40. × 20.

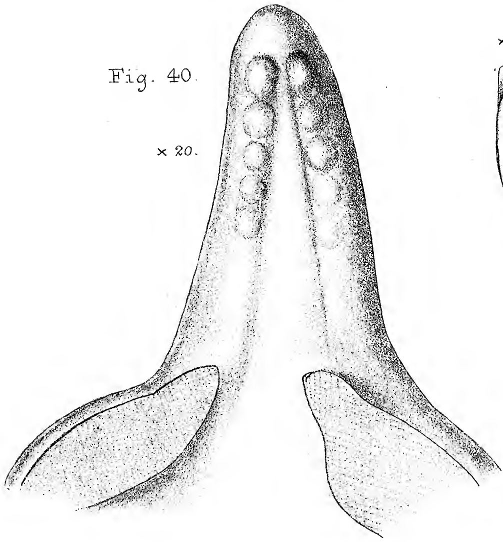


Fig. 41. × 20

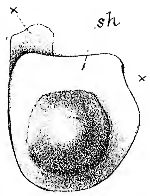


Fig. 42. × 20

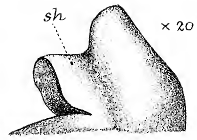


Fig. 43. × 20

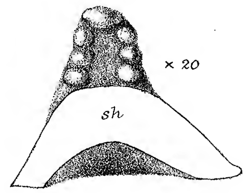


Fig. 44. × 2

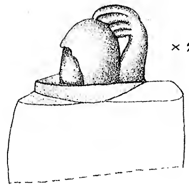


Fig. 45. × 20

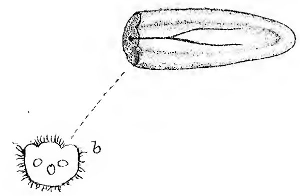


Fig. 47. × 20

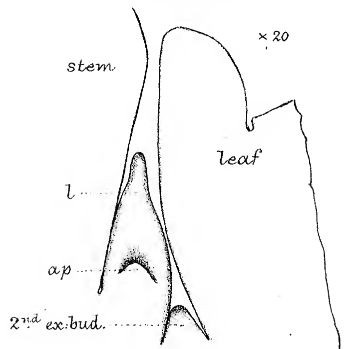


Fig. 48. × 20

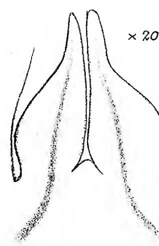


Fig. 49. × 20

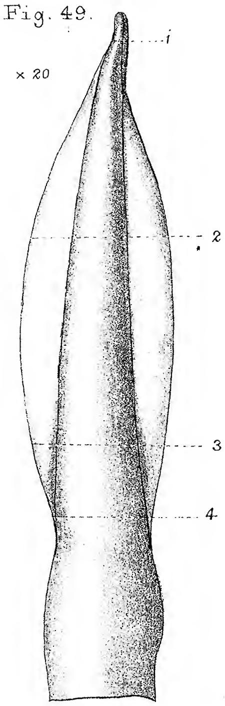


Fig. 46. × 4.

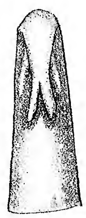


Fig. 50. × 20.

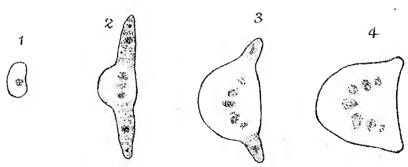


Fig. 51. × 175.

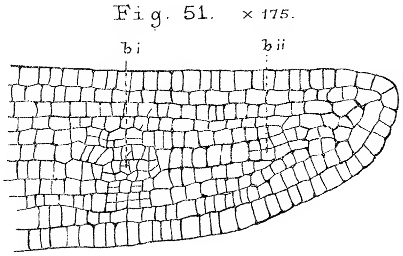


Fig. 52. × 20

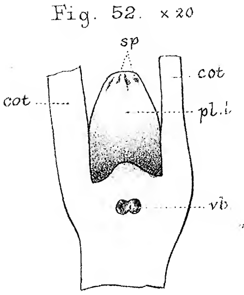


Fig. 53. × 20.

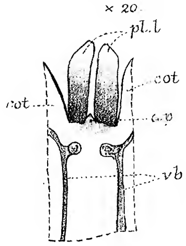


Fig. 54. × 20.

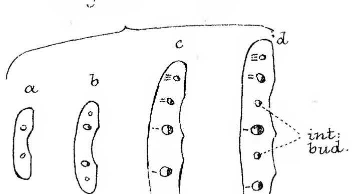


Fig. 55. × 20